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HEREDITY AND VARIATION

Continuity and Change in the Living World

By L. C. DUNN, D. Sc.

PROFESSOR OF ZOOLOGY, COLUMBIA UNIVERSITY

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To
My Wife

THE MONUMENT TO GREGOR MENDEL, FOUNDER OF THE SCIENCE OF GENETICS

At Brünn, Czecho-Slovakia, where he carried out his famous experiments

CHAPTER I

THE SIGNIFICANCE OF HEREDITY

THE study of a science which deals with the processes by which new living things come into being must be conceded to be fundamental to an understanding of life and its laws. *Genetics,* the scientific study of heredity and variation, is still a comparatively new subject, but it has already built up a body of principles which are rapidly gaining popular consideration and finding important practical applications. Intelligent people wish to know and need to know the nature of those laws by which heredity operates, not only because the laws themselves are clear and general and well established as an important part of modern science, but because *human character and behavior are themselves in part the results of the operation of these laws.*

THE NATURE OF THE SUBJECT

Interest in heredity is becoming rapidly more and more widespread. In part this is due to an increased appreciation of science and of the fact that human progress and human happiness depend fundamentally upon the application of intelligence. It is more especially the result of the rumors which have been bruited that now something real and definite is known about heredity. Whenever it becomes possible to give not stones but intellectual bread when it is asked for, there is a real and increasing demand for knowledge. It is now possible to give reasonable answers to such questions as: How are the characteristics of plants, of animals, and of men inherited? Through what mechanism are similarities preserved through many generations, and how do differences arise? How is that fundamental difference, sex, determined? What is the explanation of the results of inbreeding and of cross-breeding? What is the relative importance of heredity and environment? These and many

other questions can now be discussed without fear or prejudice. Many facts are available, theories have been built from them and tested by more facts. The groundwork of an understanding of heredity and of variation now seems to have been laid. Let us examine first the ideas and the facts which define the problems and see what is meant by the terms "heredity" and "variation."

Resemblances and Differences

Two facts about the members of the human race are patent to every observer. The first is that they are all alike; the second is that each is different. They are alike in those features which make them members of one species of hairy, backboned animals which walk on their hind legs, use tools, and indulge in talk. Men differ in thousands of minor ways—both physically and mentally. It is literally true that no two of them are exactly alike. Moreover, their resemblances reappear with great fidelity in their children. Each child repeats all the essentially "human" features of the parent, most of the racial ones, and many of the individual ones. "Like produces like" in regard to general characteristics, but only "almost like" in regard to particular ones.

The same observations may be made of any kind of animal or plant. In some sense all dogs are alike. From wolfhound to Pekingese a certain essential dogginess runs through the whole species. Wolfhound and Pekingese each perpetuates in his offspring all this dogginess; each produces the sort of progeny proper to his breed, and yet among the members of each breed appear differences in color, shape, and behavior which make each dog an individual.

In a wider sense the same sorts of resemblances and differences run through the whole living world. All animals and plants resemble each other in fundamental ways; they are built of the same stuff, organized in the same kind of units, reproduce in the same general way, and require the same general type of environment. The basis of this fundamental unity we now understand to be the *common origin* of all plants and animals. All forms of life seem actually to be related to each other, descended from the same ancestral life.

But wide differences have appeared within this unity.

Animals, for example, have become as different from each other as the minute protozoan from the whale. And all of this has taken place, we must believe, through the successive transmission

Courtesy of the Iowa State College of Agriculture

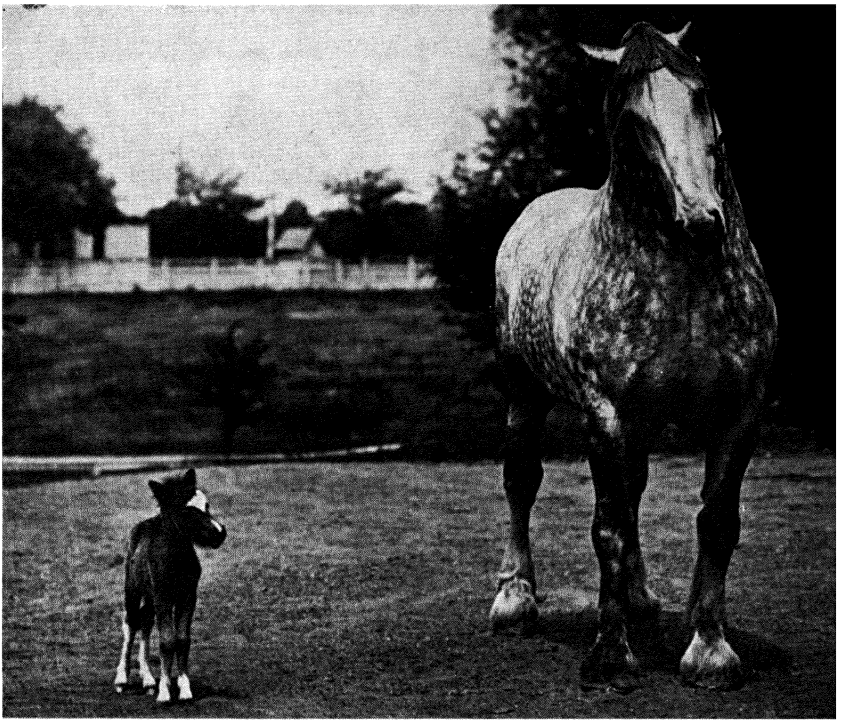


Fig. 1—EXTREME VARIATIONS IN HORSE STATURE
A Percheron draft horse and a Shetland pony colt

of life and its attributes by the same means of reproduction with which we are now familiar.

The Meaning of Heredity and Variation

As we review the continuous history of life on the earth, and as we consider the forms in which it appears today, we are struck by two great tendencies which seem to be co-extensive with life itself. The first of these tendencies is for the general characteristics of living things to be retained and transmitted to all descendants, thus producing sameness, resemblance, conservatism, and fixity of the *status quo*. This fact of resemblance is usually

known as *heredity*. The second great tendency in life is for differences to arise, for rare novelties and changes to appear. This is what the biologist means by *variation*.

Fig. 2—EXTREME VARIATIONS IN HUMAN STATURE
A giant eight feet tall and a dwarf 28 inches tall

Heredity describes for the fact of *continuity* of the characters of organisms; it is the expression of the great (but relative) stability which marks the species of animals and plants over long or short periods of time. *Variation* designates the changes which appear in the species or in the individual; any departure from the type or norm we call a variation. Some of the variations in the human species are so striking and unusual that the majority of our race which is normal (*i.e.*, having less extreme variations) will flock to the circus tent or sideshow to see them (Fig. 2). Most of us, however, differ in less obvious and more subtle ways—in physical features of size and shape and color; in habits, both physical and mental; and in those combinations of peculiarities which we call temperament, disposition, and ability. Many of these differences are obviously acquired. They appear as the result of the special conditions under which we live—our early environment, occupation, and education, and the diverse opportunities which we encounter. But many of them are inborn and in our study of heredity these variations hold chief interest.

Resemblances Are Never Quite Perfect

It is obvious that heredity is never absolute; resemblances are never quite perfect. Among the progeny of certain wheat plants appear one or a few not quite the same as the parent, but markedly superior. From these descend a new variety which represents so great an improvement that it soon displaces all other wheat varieties and changes the whole agriculture of a great area. Thus the *variation,* the novelty, itself *becomes the norm,* the stable condition, within which perhaps another rare change may take place.

The truth is that heredity itself changes, and the changed condition—the variation—is thus perpetuated with the same tenacity which marked the earlier condition. Variation in this sense is but another aspect of heredity—a defect in its perfection.

Variations, or departures from type, are the raw materials of all progress. A world in which complete and perfect repetition was the rule would be static—fixed. It could not change, and change is the very essence of the world in which we live. In the social sphere, a world in which heredity was absolute would be like a society in which every member would be identical with every other and in which no change—social, political, economic—could take place. If this had been the case, no complex civilizations like those of the present could have arisen. Variation is a primary condition of progress.

The Mechanism of Heredity

The generations of all animals and plants are joined by living links; life is perpetuated by the passage of actual living material from parent to offspring. This process is known as *reproduction,* and it is essentially similar in all animals and plants. Some mechanism in reproduction must therefore provide for the transmission of resemblances and must make it possible for new differences to arise and to be perpetuated.

The discovery of this mechanism has been one of the most notable achievements of modern biology. Beginning with the dramatic episodes centering about the name of Mendel in the latter half of the nineteenth century, springing suddenly into renewed and active life at the dawn of our own century, the

knowledge of the mechanism of heredity and variation has progressed with increasing momentum until it is now one of the most active and exciting studies in the whole field of biology. A new science—*the science of genetics*—has grown up to till this rich field. It is gradually helping to write a new biological genesis—dealing with the origins of races, species, individuals—having as its central thesis a new and unified theory of heredity which, in its general features, may be understood by any intelligent person who knows the elements of biology.

This fills a real human need, for people have always been curious about heredity. There have been the puzzles of specific resemblances and differences among the children of men which so frequently have seemed erratic and utterly mysterious. There have been the differences distinguishing the races of men—differences in color and form, in specific abilities, and in temperament. Moreover, civilized man has depended on agriculture from the earliest times, and his interest in heredity has been greatly stimulated by the practical problems which continually presented themselves to the breeder of animals and to the cultivator of crops. Not only has man's curiosity been piqued for generations, but his very means of livelihood has been faced with problems directly connected with heredity.

Heredity and Experience

Beyond all these practical considerations lie questions of greater import. Man has always recognized more or less clearly that his own character and his fate, and therefore his happiness, are the result of two forces—his *heritage* and his *experience*—the one innate, inborn, the other arising from his contact with his environment. Every philosophy has had to examine the relationship between these, and every thinking man must sometime inquire in what respect these two interplay to rule his life.

Two opposed points of view have crystallized. One is that man is a free agent—"I am the master of my fate; I am the captain of my soul." He comes into being with none of his reactions determined by heredity; his will is free, and he is therefore responsible for all his acts. Our present social, political, and religious structures are in some measure resultants of

this view. The other view is that man's acts are determined by the mechanism with which he is equipped at birth—his will is not free but bound; he is not responsible but at the mercy of the chances that determined his heredity.

Concerning these two views the modern teachings of genetics have something quite definite to say. *It has become increasingly obvious that an understanding of the evidence concerning heredity is fundamental to any philosophy of life.*

Genetics a Fundamental Science

Genetics is now in a position to satisfy some of the demands for help and understanding which have been accumulating from the age-long interest in heredity. Farmers now recognize it as one of the sciences of the first importance to agriculture. The permanent improvement of stock and crops depends fundamentally upon the ability to manipulate the heredity of our cultivated animals and plants within the best environment which can be provided. It is quite plain that improving the soil or food (*i.e.*, environment) exerts no permanent effect; this must be repeated in each generation. But permanently superior varieties of animals and of plants can be produced by proper breeding. The successful breeder has done it in the past. With the aid of the newer knowledge of heredity the breeder of today is able to do it more rapidly and more efficiently.

Making Use of the Knowledge of Heredity

The knowledge of laws of inheritance is making possible a much more rational viewpoint concerning the heredity of human traits. It is even possible in some cases to predict the character of offspring from a knowledge of the parents, and *vice versa.* The mode of inheritance of many human characteristics, both physical and mental, has already been worked out, as well as the part which heredity plays in specific diseases and defects.

It has been proposed to put this knowledge to work in an effort to avoid the continuance and multiplication of many hereditary defects, and the applied science of *eugenics* as an agency for effecting such improvements has grown up side by side with genetics. It has become obvious that all programs of

social improvement must be based on a thorough knowledge of human heredity and that this should be a part of the general knowledge of all citizens. Here the ramifications of the newer theories run wide and deep, for they penetrate and color our viewpoints concerning marriage and the interminglings of races, immigration, and population, and the fundamental questions of war and peace with which the world must more and more concern itself.

Some of the Problems

The application of our knowledge in many of these instances is indirect. We can have confidence in what we know of man only in so far as it coincides with what we know of the general laws which govern all animals and plants. More and more, biology conceives of life as a whole and judges the importance of its problems by the degree to which they embrace the whole living world. One of its central problems concerns the methods by which the species of animals and plants change and adapt themselves to their environment.

The origin of new species by slow processes of descent with modifications from older species which we call *evolution* is a patent fact, but the *mechanism* by which this occurs must be demonstrated before we can say that we really "understand" evolution. It is obvious that new variations arise, some of which persist and thereby change the species, whereas others do not. The heart of the problem is to discover how these new heritable variations arise, how they are inherited, and how they fit the species to cope successfully with its environment.

It is because genetics has thrown a flood of new light on the second of these problems—how characters are inherited—and is now beginning to elucidate the first—how new characters originate—that it assumes so important a place in biology, and enters into all considerations of the origin and development of life on earth. Evolution and development and perhaps all biological theories are historical ideas, since they deal with systems which change with time, and many thoughtful people are now realizing that history has a future as well as a past and are turning their attention to the effects which these ideas are likely to have upon human conduct and behavior. Through such

channels the theories of genetics have an indirect but important bearing on scientific thought and therefore on human culture.

Life Follows Natural Laws

Finally, one of the most interesting and important results of modern research on heredity has been to show that in this domain of biology *living things follow exact and orderly natural laws*. For heredity this is easy to demonstrate; the experimental evidence is neither difficult to obtain nor to understand. It thus acts as a confirmation of our faith in natural laws, and helps to make of this world, which so often seems a topsy-turvy and illogical aggregation of events, a more orderly, a more homelike, and a more reasonable place. Concerning the physical units of which life is built we now have reasonable ideas. The genes, or factors, by which inheritance takes place seem to be such units. In order to understand life we must know what these units are and how they operate, just as the inorganic world has to be understood in terms of the atom and the electron. To record some of the progress represented by the attainment of such ideas is the chief function of this book.

CHAPTER II

REPRODUCTION AND HEREDITY

Passing of Old Ideas

Ancient ideas about heredity seem absurd to us because there were no sensible or tested ideas concerning reproduction and the sexual process upon which heredity in all the higher animals and plants depends. Aristotle, the greatest biologist of antiquity, whose ideas ruled natural philosophy until the sixteenth century, included among the methods of reproduction the spontaneous generation of animals from dead matter. The idea of spontaneous generation avoided or abolished the chief problem of heredity, which is to discover how the characteristics of the parents are distributed to the offspring, since under spontaneous generation there was, properly speaking, no parent and no offspring.

The relationship of the sexes in producing the new generation was also for long unknown. Among the higher animals it was obvious that the origin of the new individual depended on the combination of certain contributions from each parent, but the nature of these contributions and the equal importance of each in reproduction was not known. In plants the sexual process itself, as the union of a male cell in the pollen grain with the female egg in the ovule from which the seed arises, was not clearly recognized until the middle of the eighteenth century.

The most important ideas ancestral to the modern theory of heredity were, therefore, those concerned with elucidating the exact method of reproduction. The chief facts on which agreement had to be reached were: (1) There is no spontaneous generation; every living thing has a parent—*Omne vivum ex vivo* (all life from previous life). (2) Animals and plants consist of units of protoplasm known as cells, and multiplication and reproduction of life takes place by division of the cells. (3) Sexual

reproduction consists in the production by the parents of single reproductive cells (egg and sperm) from the union of which the new individual arises.

The old notion of spontaneous generation died a slow and lingering death; it was finally slain and interred by Pasteur, whose dramatic experiments in the second half of the nineteenth century showed that it could not even apply to the microscopic yeasts and bacteria which he had discovered.

Together, the microscope, the experiment, and the willingness of men to derive their ideas from an appeal to nature itself began to banish the fog which had obscured so many of the essential facts of life and made it possible to see more clearly the why and how of such seemingly hopeless riddles as heredity.

New Ideas and New Discoveries

Biologists now have a theory of heredity. Formerly they had many theories, which, in science is equivalent to saying they had none. *Scientific theories are condensed statements of experience,* and when theories become fewer and more unified it means that much experience converges toward confirmation of a few general ideas in which we gain more and more confidence. This change toward unity and agreement is one of the best indications of real progress.

What wrought this transformation in our ideas of heredity? The materials of experience are much the same for men of all times. The reappearance of traits of the parents in their offspring and the differences between individuals and races have been patent facts since man first began to observe his fellows and the animals and plants about him. They are especially apparent in the animals and plants which have been domesticated and upon which every civilized society has depended; and yet such observations did not lead to any general or satisfactory theories of heredity until the beginning of the present century.

We cannot find the answer to this question by examining merely the history of genetics or of biology, for modern scientific theories could not be built until a great liberation of the mind took place and it became free to draw its ideas directly from the evidence of nature as gained through the senses. Even after Bacon, Galileo, and Newton had pointed the way to the dis-

covery of natural laws and had thus threatened the reign of magic and superstition and supernatural law in the physical world, progress in biology had still to wait upon the development of new methods of observation.

Of the greatest importance were, first, the discovery of the method of *experiment,* by which ideas concerning living processes may be rigidly *tested* in an artificial, man-controlled model; and second, the invention of the *microscope* which led eventually to new knowledge of how animals and plants are built and especially of how their reproduction takes place. The experimental method is now the most reliable guide to correct conclusions and all biology has come to depend upon it for its progress.

The Continuity of All Life

The full significance of this would not have been apparent, however, without the realization, which had been slowly growing in the minds of biologists, *that all living things are composed of the same sort of stuff*—a semi-fluid substance composed of many of the common elements, united into a working system which can carry out those remarkable activities which we call *living.*

This substance became known as *protoplasm,* the true physical basis of life. During the first half of the nineteenth century the labors of many investigators, who were applying the still novel and imperfect microscope to the study of the tissues of animals and plants, converged in showing that protoplasm is always organized into minute working units, each consisting of a dense central portion known as a *nucleus,* together with some less dense and more fluid *cytoplasm* which surrounds it. Such an organization became known as a *cell,* from a mistaken analogy with little boxes or the cells of a honeycomb which it superficially resembles. This sort of unit was found in all living things.

Some animals and plants—protozoa, yeasts, bacteria—consist each of a single cell, while the larger forms of life consist of vast numbers of these minute units. In the adult human body there are actually thousands of millions of them, aggregated through their co-operative activities into a higher unit of organization—the individual. Cells vary in details of structure and function according to the special activities of the organs and tissues which they form, but all are alike in their fundamental organization,

and even specialized cells taken from the body of a higher animal can perform the functions essential to life, since, if provided

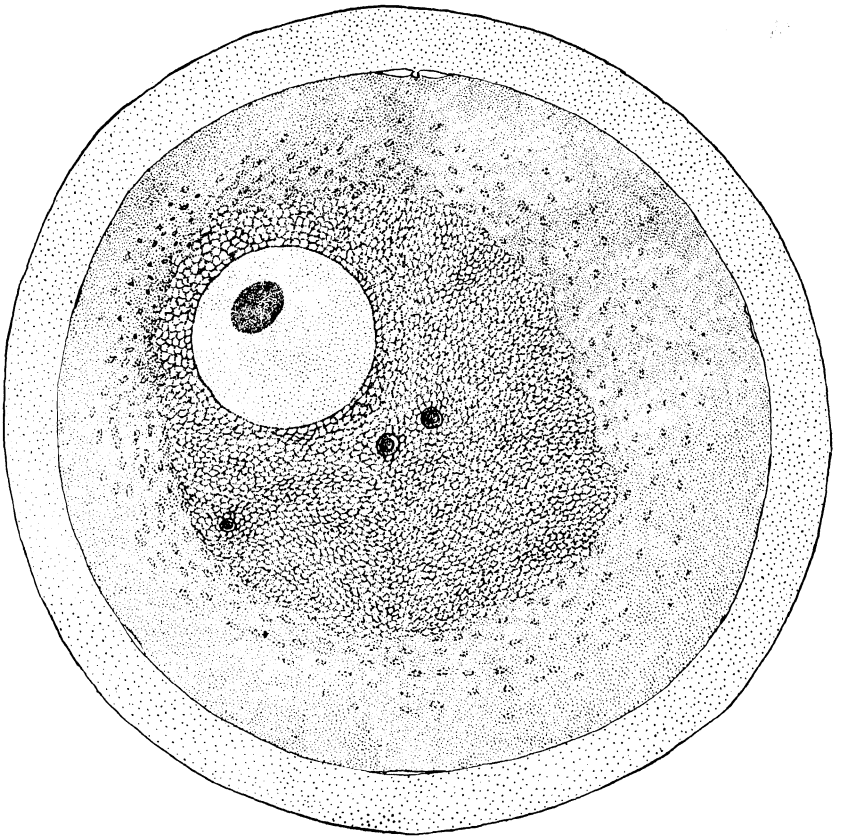


Fig. 3—HUMAN EGG AND SPERM
Magnified 375 diameters
After Hertwig

with proper food and guarded from infection, they can live indefinitely.

The Importance of This Discovery

The revolutionary nature of this discovery of the cellular basis of life can best be understood by considering the light which it threw on reproduction. Living things were found to increase in mass and grow by division of the cells which compose them.

All multicellular animals and plants, however, reach at some time a limit of increase in size. Sooner or later they grow old and die. None is immortal. But before death ensues they give rise to new individuals like themselves by separating from their bodies some cells which have the remarkable power of beginning life over again.

The Essential Nature of Sexual Reproduction

In the vast majority of animals and plants reproduction consists in the preparation by the parents of single reproductive cells, the *gametes*. The essential nature of sexual reproduction was found to consist in the production of two different types of gametes: (1) the egg—a large cell with a single nucleus and usually much cytoplasm and stored food (yolk); (2) the sperm or male cell, usually motile, active, and containing little besides a nucleus and accessory structures to help it find and enter the female cell. These sexual cells are extremely small. In man it has been estimated that all of the eggs from which the present population of the world arose could be contained within a two-gallon jar, while the billion and a half of sperm which fertilized these eggs would occupy no more space than that represented by two pin heads. (Fig. 3.)

Both types of cells are produced in the bodies of the parents by a series of cell divisions, and thus the offspring which arises from the fusion of the two single cells—egg and sperm—receives a bit of the actual living substance of its parents. Although a few kinds of animals and plants reproduce *asexually*, as by simple fragmentation of the parent body, in all of them the offspring is a physical continuation of the parent. New individuals arise only by this passage of living protoplasm from parent to offspring. So far as we know, the living substance can only arise from pre-existing life.

The implications of these discoveries were so vast as to completely transform our conception of life. Thenceforth life had to be conceived as a continuous stream of living substance connecting all living things both in time and space. All animals and plants must thus have had a common and single origin and the later ones must be descendants of the earlier. About the middle of the nineteenth century the methods by which this might be

conceived to have occurred were embodied in Darwin's theory of the differentiation of species by natural selection.

The process by which cells divide and by which the gametes or sexual cells are formed will be discussed in more detail in Chapter IV. At present it is most important to recognize how essential the discovery of the general nature of sexual reproduction was to an understanding of the methods by which the characteristics of the parents pass through the single cells which constitute the sole living link or bridge between the generations.

Some Early Clues to the Riddle of Heredity

Some of the first clues to the riddle of heredity were obtained by the early microscopists at the end of the seventeenth century when the male sex element of animals—the sperm or spermatozoön—was discovered. The female element, or egg, was not correctly demonstrated until more than a century later, nor did the essential nature of sexual reproduction as the preparation by the parents of single marrying cells, or *gametes,* and of the union of these single cells to form one cell from which the whole new individual arises, become clear until the latter half of the nineteenth century. Indeed there raged among the microscopists of the eighteenth century a battle which now seems amusing, for it was based on the assumption that either the sperm or the egg was a tiny replica of the complete adult individual compressed within the reproductive element. The bitter argument was whether it was the sperm or the egg which contained this little individual. Just as by a sufficient use of the imagination we think we can discover a man in the moon, so these ardent observers descried an *homunculus*—a little man complete except for size—within the sperm. The whole argument evaporated when, with improved technique, the sperm and the egg were each shown to be single cells.

Sex in Plants

In higher plants the function of the pollen grains with the male cells which they contain and the ovules which produce the egg and later the seed began to be recognized from experimental evidence during the eighteenth century, for by putting pollen from one species on the flowers of another it was shown that the

hybrids were intermediate and that the hereditary characters were transmitted equally through the tiny pollen grains and through the tissues (now known to be the eggs) of the mother-plant. In these experiments the nature of fertilization as the union of unlike sexual elements was clearly recognized for the first time in plants, and this bit of knowledge was necessary for the later experiments with plants which led to the discovery of the laws of heredity. Even here, however, the unicellular nature of the gametes was not established until much later.

Expansion of Knowledge

The latter part of the nineteenth and the early part of the present century saw a remarkable expansion in knowledge of the finer structure of cells and this gave rise to a new branch of biology—*cytology,* or the study of cells. Attention soon centered on the nucleus as the governing center of the cell and the part chiefly concerned with reproduction and heredity. The nucleus was found to contain still smaller organized bodies—the *chromosomes*—which appear in pairs, the number of which is constant for any species, but which vary in shape and size and number in different species.

When the cell divides, each chromosome is seen to duplicate itself exactly, and this was soon recognized as the essential feature of reproduction. The regularity and order which marked the behavior of these tiny bodies indicated that they must have some vital significance for the life of the individual and the species. Especially was this true of the divisions leading up to the formation of the gametes, for it was found that into each sexual cell went regularly one representative of each pair of parental chromosomes. Thus to the continuity of protoplasm and of cells was added the continuity of each individual chromosome.

The one fact that fertilization consists in the union of two single cells (this was recognized by the middle of the nineteenth century) was alone sufficient to pose the problem of heredity in a new light, *i.e.,* to explain how the characters of the parents passed through the gametes and reappeared in the offspring. This realization was itself sufficiently startling, for it meant that the whole heredity of complex animals and plants had to pass

through two cells of almost inconceivably small size. That many unsuccessful attempts at a solution were made even after this prime fact was recognized indicates that knowledge of the reproductive mechanism alone was not sufficient.

Attempts to Find a Solution

There were, for example, several unsuccessful attempts to construct a theory of heredity based on the transmission of some kind of units through the reproductive cells. The theories of Darwin, of Spencer, and of Weismann were of this character, but these scientists were unable to determine how these units got into the germ cells, or what characters of the organism they affected, for their theories were not in general based on the experimental evidence necessary to test these points.

Weismann came nearest to solving the riddle by assuming that the chromosomes of the germ cells carry determiners for the various characteristics of the body. He effectively disposed of Lamarck's supposition that the direct effects of the environment might become heritable, not, as is often supposed, by the rather naïve experiment of cutting off the tails of mice for many generations, but by showing that in many animals the tissue which is to form the gametes (the germplasm) is put aside for this purpose early in life and is not in general affected by accidents which befall other parts of the body. The uniting gametes are assumed to produce the cells of the body, or soma, and also to produce directly new germplasm like itself, which is thus continuous or immortal, whereas the body, a by-product, dies without leaving any mark on the germplasm. Samuel Butler's epigram puts Weismann's case into a nutshell: "The hen is only the egg's way of making another egg." In the identification of the germplasm with the chromosomes of the gametes and in the ascription of hereditary differences to different combinations of hereditary elements in the chromosomes Weismann foreshadowed several of the ideas in the modern theory, without, however, supplying the chief or fundamental idea which easily differentiates all of these unsuccessful theories from the one which now seems to be true.

Botanists who were studying experimentally the results of crossing different species and varieties of plants had in the mean-

time hit upon the track which led to success, for they had discovered the equal transmission of traits from both pollen and seed parents, and had observed that hybrids in their further breeding tend to produce again the parental forms which had gone into their composition. This "splitting" of hybrids appeared to concern the whole complex of characters by which the parent species differed, as though hybrids could form germ cells of two sorts, each carrying the potentialities of the species from which the hybrid came.

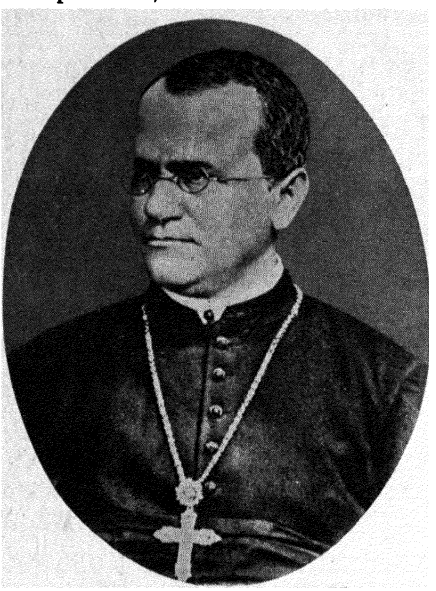


Fig. 4—GREGOR MENDEL
1822-1884
Discoverer of Mendel's Laws of Heredity

Mendel and His Work

The eventual solution came when one man took a new and different view of the whole problem of heredity and applied to it a unique method of analysis. It came from an unexpected source, for while the leaders of biological thought were concerned with the broad question of evolution and the origin of species, while they were building speculative theories of the manner in which heredity might be explained, an ardent student in an Austrian monastery was quietly performing the careful and detailed experiments which finally solved the riddle. This student was the Augustinian monk, Gregor Johann Mendel, who succeeded where others had failed because he alone devised a new method, carried it into execution with thoroughness, and brought to the analysis of his results a mathematical or statistical insight which at one stroke brought order out of chaos. The story of this man's work, of the neglect which it suffered and of its eventual recognition long after his death, is one of the most astonishing in the history of biology. The next chapter will recount it in detail.

CHAPTER III

MENDEL'S DISCOVERY

THE story of Mendel's discovery contains all the elements of a good drama. After long pondering of botanical literature this humble monk in a Moravian monastery decides that "no generally applicable law" of heredity has been formulated and he deliberately sets out to discover this law. From the beginning Mendel recognizes the audacity of this project and the persistence required to carry it through, but, like a true scientist, he never doubts that such a law exists and that it is his duty and pleasure so to frame his questions that nature cannot fail to answer them.

THE QUESTIONS AT ISSUE

Deliberately he states for the first time the questions at issue: (1) To discover the *number* of different types which appear when plants with different characteristics are crossed; (2) To discover the *numerical ratios* in which these types occur in the various crossbred generations. Deliberately he chooses the material to be used in the investigation—the common pea plant. He invents a method by which the ancestors and offspring of every individual plant can be distinguished, formulates a detailed plan for the experiments, and painstakingly proceeds to carry it through.

He fills the monastery gardens with races of peas which he has collected from seedsmen; tall peas and short peas, peas with purple flowers, peas with white flowers, smooth-podded peas, crinkly-podded peas, peas differing in the shape and color of the seeds—all the varieties of peas which he could get. He carefully tests these varieties by breeding them for several generations and selects only those which breed true. He then makes crosses among these races, painstakingly placing the pollen of one sort

on the pistils of the other, describes every plant produced and guards against the continual errors which tend to creep into every experiment.

He is doing all these things for the first time, yet in all his plans and in their execution we can today discover no flaw, nothing the modern experimenter, after years of intensive experience with the same sort of problem, would change. Finally, in 1865, at the end of eight years of work, Mendel recounts the story of his experiments simply and briefly before the meetings of the *Natur-Forschender Verein* (the Nature-Searching Society) in Brünn, and prepares a paper of some forty-odd pages which is published in the proceedings of this society in 1866. In this single paper, in language which is a model of simplicity and conciseness, Mendel gives the results which he had obtained, and his explanation of them. This explanation, in fact, constituted the very laws, or principles, of heredity which he had sought.

After the publication of these results—the rest is silence. They appear to have made not the slightest impression on the science of the times. The paper was duly laid on the desks of many botanists and filed in the archives of a number of learned societies and there it remained unnoticed for thirty-four years.

There is no doubt that the Gregor Mendel of 1866 recognized the epoch-making significance of his work, nor could he conceal his disappointment at the lack of comprehension which it encountered. He continued his scientific work, however, but further disappointments were in store for him. In 1868 he was chosen abbot of his monastery and soon after he entered into a bitter and protracted struggle over the taxation of the extensive estates of the cloister. Mendel threw himself whole-heartedly into this battle and, as his "righteous cause" gradually lost, his life became embittered and he died in 1884 a broken and unhappy man.

Confirming Mendel's Work

It is, to say the least, unusual for an idea of such importance to be discovered in such comparative obscurity and to remain completely unrecognized for so long a time, but the suddenness with which it finally burst upon the world and the revolution in biological science which it wrought were more unusual still. As

though to make amends for long neglect, three botanists, De Vries in Holland, Correns in Germany, and Tschermak in Austria independently and almost simultaneously, obtained results similar to those of Mendel and in 1900 "rediscovered" Mendel's work. It was instantly recognized as unique and

Versuche über Pflanzen-Hybriden.

Von

Gregor Mendel.

(Vorgelegt in den Sitzungen vom 8. Februar und 8. März 1865.)

Einleitende Bemerkungen.

Künstliche Befruchtungen, welche an Zierpflanzen desshalb vorgenommen wurden, um neue Farben-Varianten zu erzielen, waren die Veranlassung zu den Versuchen, die her besprochen werden sollen. Die auffallende Regelmässigkeit, mit welcher dieselben Hybridformen immer wiederkehrten, so oft die Befruchtung zwischen gleichen Arten geschah, gab die Anregung zu weiteren Experimenten, deren Aufgabe es war, die Entwicklung der Hybriden in ihren Nachkommen zu verfolgen.

Dieser Aufgabe haben sorgfältige Beobachter, wie Kölreuter, Gärtner, Herbert, Lecocq, Wichura u. a. einen Theil ihres Lebens mit unermüdlicher Ausdauer geopfert. Namentlich hat Gärtner in seinem Werke „die Bastarderzeugung im Pflanzenreiche" sehr schätzbare Beobachtungen niedergelegt, und in neuester Zeit wurden von Wichura gründliche Untersuchungen über die Bastarde der Weiden veröffentlicht. Wenn es noch nicht gelungen ist, ein allgemein giltiges Gesetz für die Bildung und Entwicklung der Hybriden aufzustellen, so kann das Niemanden Wunder nehmen, der den Umfang der Aufgabe kennt und die Schwierigkeiten zu würdigen weiss, mit denen Versuche dieser Art zu kämpfen haben. Eine endgiltige Entscheidung kann erst dann erfolgen, bis Detail-Versuche aus den verschiedensten Pflanzen-Familien vorliegen. Wer die Ar-

1*

Fig. 5—A PAGE FROM THE ORIGINAL PAPER OF MENDEL

The copy from which this photograph was made is owned by Columbia University

fundamental, and within a few years his ideas had been so confirmed and extended, not only for the plant with which he had worked, but with so many species of animals and plants and even for man himself, that it became increasingly evident that here was a truth so general that it applied to the whole world of living things.

The Man and His Ideas

There is nothing in the ideas nor in their author to account for the dramatic events which make up the history of the discovery and rediscovery. The ideas themselves are essentially simple, and the man himself was an unassuming scientist with not a trace of self-consciousness whose sole interest lay in establishing the truth of purely scientific ideas. There is no embroidery whatever in Mendel's paper; by its very nature it can appeal only to the reason and to that esthetic sense which recognizes and appreciates the beauty of a structure of ideas which, like a good building, provides on its face the reason for its creation. The romantic element inheres in the contrast between the man and his ideas on the one hand and the time and place against which they were projected on the other.

The Nature and Results of Mendel's Discovery

The essence of Mendel's discovery is that inheritance seems to consist in the passage through the reproductive cells from one generation to the next of separable units which affect the development of specific characters of the organism. This idea was an inescapable conclusion from experiments and can best be made clear by recounting some typical examples from breeding experiments.

Suppose we choose two pure breeding varieties of animals differing in some easily distinguishable character, and cross a male of one variety with a female of the other. For example, let us cross a black cock from a variety known as the Andalusian fowl with a white Andalusian hen—or *vice versa* (Fig. 6). The cross-bred or hybrid chicks produced from this mating are all *slate blue,* a color apparently intermediate between those of the parents. When these blue chicks reach maturity they are mated to each other, and among their progeny are found chicks of three

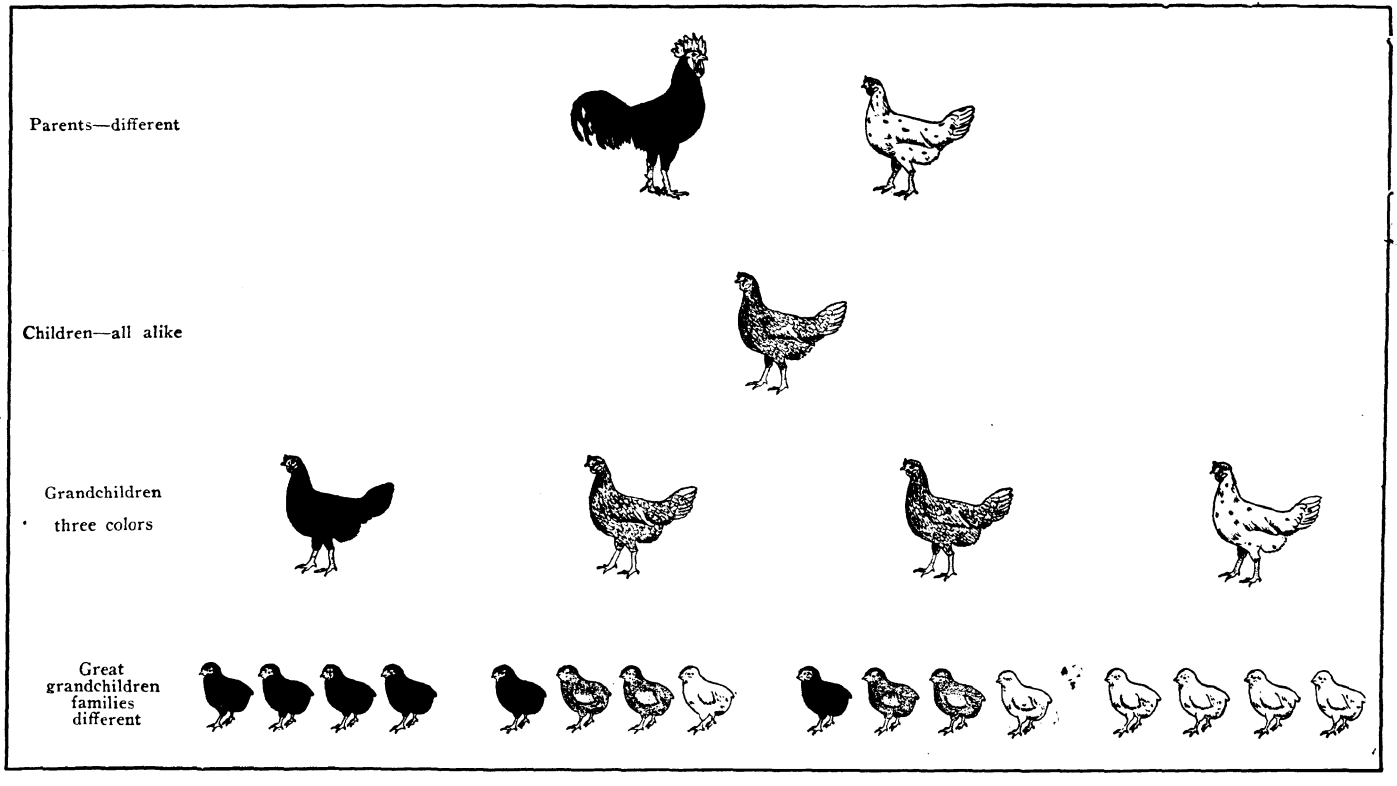


Fig. 6—INHERITANCE OF PLUMAGE COLOR IN ANDALUSIAN FOWLS

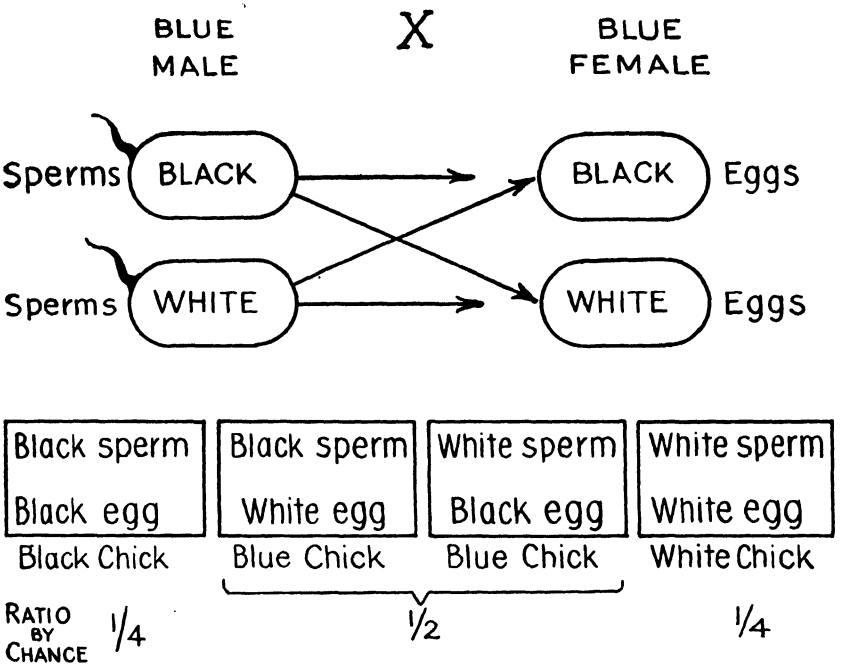
From a drawing by the author

sorts: some of them are blue like the parents, some are black like one grandparent, and some are white like the other grandparent. Let us now follow Mendel's lead and *count* the numbers of these different types in the second generation.

In large numbers of experiments it is found that about one-quarter of these chicks are black, about one-half of them are blue, and about one-quarter are white. If we breed these black chicks together they produce only blacks—they constitute a "pure" race like that from which the black grandparent came; the white chickens bred together produce only whites—they also are "pure" for white; whereas the blues bred together produce again blacks, blues, and whites in the ratio of $\frac{1}{4}$: $\frac{1}{2}$: $\frac{1}{4}$. Black and white have apparently been inherited through two generations and have not been changed even by their passage through the blue or hybrid condition.

In explaining this occurrence, which is a regular feature of Mendelian inheritance, it is necessary to recall first that each chicken received from its father a single minute sperm cell and from its mother a single cell nucleus in the egg. Whatever characteristics it exhibits must somehow have come through these single cells.

Let us assume that all the sperms of the black male contain something that stands for black. Let us call this purely arbitrary something a *unit-factor,* or *gene.* In every egg of the white mother let us assume a gene for white. When these unite in fertilization, the new individual has a pair of unlike genes, one for black and one for white in each cell of the body. If we wish we may assume that these genes compete for expression, and that neither is completely successful. The result is a draw, and an intermediate effect—neither quite black nor quite white—is the outcome. The most interesting thing about these blues, however, is that they produce chickens of three *different* colors. This must mean that their eggs and sperms are not all alike. If we assume that half of the gametes of a blue fowl carry the white gene and half carry the black gene, and that one sperm is as likely as any other to fertilize any egg, then the possible types of fertilization when the blues mate with each other are as follows:



The results expected from these assumptions are exactly the results obtained in actual experiments; the assumptions "explain" or fit the results.

The Principles Involved

These were the assumptions originally made by Mendel and they involve the following principles:

(1) The representation of characters of the animal or plant by unit-factors, or genes, which pass unchanged through the gametes.

(2) The sharp cleavage, or *segregation,* of unlike genes when the hybrid forms its gametes and the passage of only *one* of them to each gamete; or to say it otherwise—half of the gametes of the hybrid receive one member of a pair of genes (such as white) and half receive the other member (such as black). This principle of the *segregation of the units* is the most important and original contribution of Mendel and it forms the groundwork for the whole theory of the mechanism of heredity.

Every gamete has thus only two alternatives—either it con-

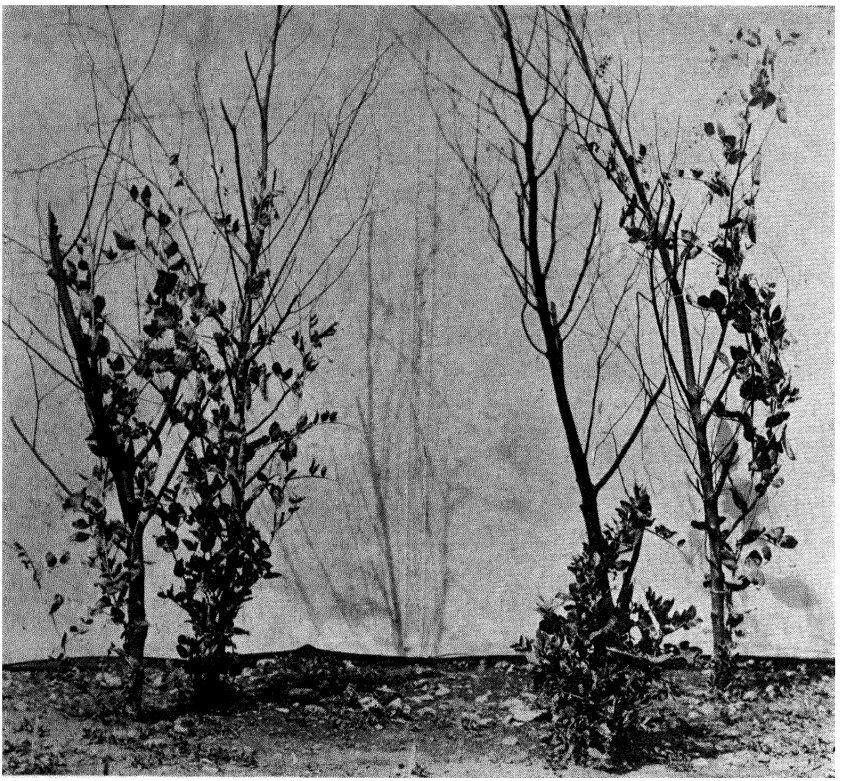


Fig. 7—TALL AND DWARF PEA PLANTS

These differentiating characters were among the first which Mendel studied. The photograph shows the segregation of three tall to one dwarf, the ratio from which Mendel established the principle of segregation

From a photograph by Dr. Orland E. White

tains a given gene or it does not. On Mendel's assumption there is no such thing as a hybrid or mixed gamete. It is always "pure." The conception of the gamete as a single structure and of the individual as a dual or double structure (always with paired genes) is in striking accord with the evidence of the microscope obtained since Mendel's time.

In his experiments with peas, Mendel found that when plants differing in a single contrasted pair of traits (such as tallness *versus* dwarfness) were crossed, the characters segregated sharply from each other in the second generation, and that dwarfness, for example, reappeared in one-quarter of the grandchildren and bred perfectly true when dwarfs were again bred

together. He discovered, however, that the hybrid is not always intermediate between the parental types in respect to the pair of characters compared but may resemble one almost exclusively. Thus tall plants crossed with dwarfs yielded only tall plants; purple-flowered plants crossed with white-flowered ones gave only purple-flowered hybrids, etc. He called this greater resemblance of a hybrid to one parent the *dominance* of the character in question. The character which disappeared in the hybrid he called the *recessive*. Mendel supposed that this was a general feature of inheritance since all seven pairs of contrasted characters which he studied behaved in this way. However, subsequent experience has shown that dominance is not the general rule, since both contrasted characters may influence the development of the hybrid and make it more or less intermediate. The essential thing is that whatever the appearance of the hybrid, the individual pairs of characters emerge from the cross just as they went in; they *segregate* cleanly and sharply.

Characters which behave in this way have now been studied

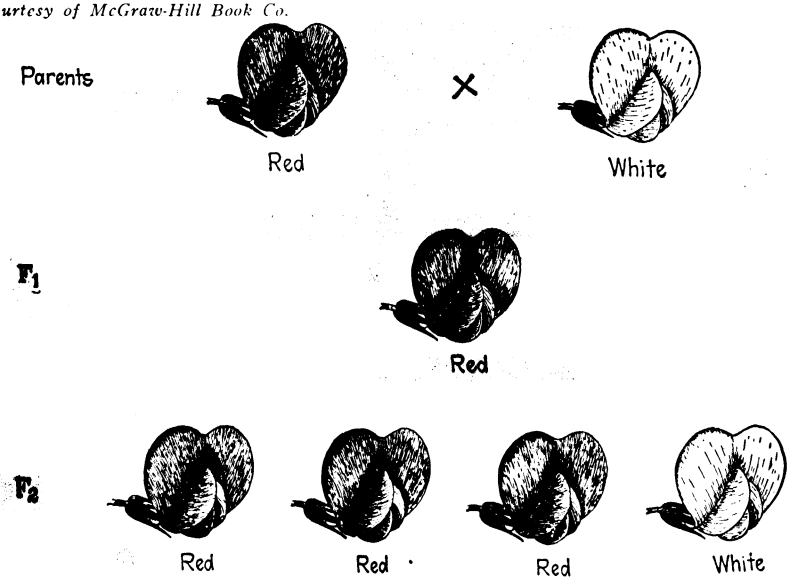


Fig. 8—INHERITANCE OF A DOMINANT CHARACTER IN PEAS

Cross between a pure red-flowered and a white-flowered pea plant, showing the dominance of red flower color in F_1. If an F_1 plant is self-fertilized the resulting F_2 generation is three-fourths red-flowered and one-fourth white

experimentally in animals and in plants from the lowest to the highest (Fig. 8). In fact, it may safely be said that *the general method of inheritance is the passage from one generation to the next of segregating units (genes) which affect the development of the hereditary characters.*

The Facts of Experience

Already from this necessarily technical description several facts of common experience begin to appear in a more reasonable light. One is, that the constancy with which the traits of parents appear in the offspring is due to the continual passage of like genes from generation to generation. The genes, like the atoms of the chemist, appear to be stable units which enter into various combinations but always come out of these combinations as they go in. They are the true conservatives of the biological world, and their stability accounts for the continuity and tenacity of type which characterizes animals and plants. But their stability is relative, for rarely a gene changes and becomes something slightly different—a black gene must sometime have produced a white one, otherwise all fowls would have only black genes, which is not the fact. Such changes in genes must be one of the prime causes of variation, or the appearance of differences. Changed genes produce variation, not only by segregating into new pure types, as in the white fowl, but by making possible new combinations, such as the blue type.

Moreover, we have learned by experience that living things are not always what they seem to be. Because of dominance, the character of the reproductive cells and therefore of the progeny cannot be predicted merely from the appearance of the parents. Now in man, brown eyes are dominant over blue, and thus some brown-eyed parents have only brown-eyed children, while other brown-eyed persons have both brown-eyed and blue-eyed children. The latter kind are, of course, really "hybrids" although they cannot be distinguished by appearance alone from the true breeding browns. In the past the animal breeder has often been fooled in buying his stock on appearances only. Now he is forewarned and demands a pedigree, or knowledge of the animal's ancestry, and if he knows the essence of Mendelism he may even demand evidence of the type of progeny which an animal has

produced, since this gives an indication of the kinds of gametes which it produces.

Recessive genes may be carried on through a stock for generations and only appear in the progeny when by a proper mating two recessive genes are brought together. When the recessive genes produce such bad effects as sterility, susceptibility to disease, physical malformation, or, as in man, feeble-mindedness, the problem of avoiding or eliminating such defects receives a rational guide from our knowledge of the behavior of genes in inheritance.

Inheritance of Two Characters

We have spoken so far only of single units, but no actual case of inheritance can conceivably involve only a single pair of units. Often only a single pair is *observed,* and it was due to such concentration on single aspects of the organism and neglect of others that Mendel was able to recognize the existence of units. Much experience indicates that all inheritance is by units. In every act of reproduction hundreds of these genes are transmitted, genes concerned with every aspect of life. How do the genes behave in combination? How are they distributed to the gametes when more than one pair of contrasting characters are followed through the generations?

Let us turn for an example to a favorite subject for experiments in genetics—the house mouse. This animal breeds rapidly in captivity and many variations have occurred in coat color, habits, and in other respects. The gray color of the wild mouse behaves as a simple dominant to the white coat of the albino. The normal running gait of the wild mouse also differs by a single dominant gene from the peculiar dancing gait of the so-called waltzing mouse. Such waltzing mice have been bred pure for centuries in the Orient and more recently in other parts of the world. They seem to be very different from ordinary mice, for their continual erratic whirling movements indicate some lack of control or fault in their balancing mechanism, and yet when crossed with normal mice the first generation is quite normal, whereas in the second generation one-fourth of the animals are typical waltzers, showing that only one gene is involved in this difference.

If we follow these two differences in heredity, we discover the laws governing the combinations of characters. The cross of a normal gray mouse with an albino waltzer produces all normal grays. When these grays are bred together we find among the progeny the grandparental types, gray runners and albino waltzers, and in addition two new sorts—gray waltzers and albino runners (Fig. 9). About three-fourths of the total are gray and about one-fourth are albino; also about three-fourths of the total are runners and about one-fourth are waltzers; and when we count the combinations we find that of the grays about three-fourths are runners, so that the gray runners comprise $\frac{3}{4}$ of $\frac{3}{4}$ or $\frac{9}{16}$ of the whole progeny; about $\frac{3}{16}$ ($\frac{1}{4}$ of $\frac{3}{4}$) are gray waltzers; of the albinos about $\frac{3}{4}$ also are runners, so the albino runner group is about $\frac{3}{16}$ of the total ($\frac{3}{4}$ of $\frac{1}{4}$), whereas about $\frac{1}{4}$ are waltzers, so that $\frac{1}{4}$ of $\frac{1}{4}$ or $\frac{1}{16}$ of the total have both recessive characters—albino and waltzing gait. The whole progeny then looks like this:

$\frac{9}{16}$ Gray runner (both dominant genes)
$\frac{3}{16}$ Gray waltzer (one dominant gene)
$\frac{3}{16}$ Albino runner (one dominant gene)
$\frac{1}{16}$ Albino waltzer (no dominant gene)

This result was first obtained by Mendel when he crossed pea plants with round yellow seeds with others having wrinkled green seeds. The hybrids all showed the dominant characters round and yellow, but in the next generation the following types appeared in these proportions:

315 round and yellow ..... (about $\frac{9}{16}$)
101 wrinkled and yellow ..... (about $\frac{3}{16}$)
108 round and green ..... (about $\frac{3}{16}$)
32 wrinkled and green ..... (about $\frac{1}{16}$)

One further assumption was necessary to explain this result, *i.e.*, that when the hybrid forms its gametes, the contrasted pairs of genes are assorted independently of each other, each gamete getting one (and only one) member of each pair regardless of its constitution in respect to any other pair. This is most readily

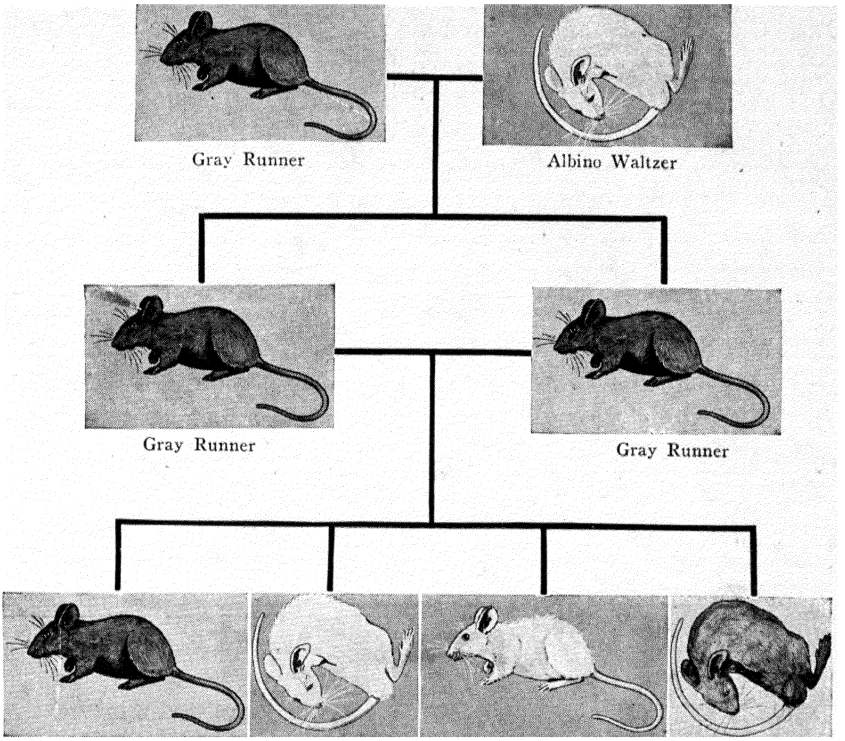


Fig. 9—INHERITANCE OF TWO INDEPENDENT CHARACTERS IN MICE

From a drawing by Mabel B. Little

demonstrated by crossing one of our gray normal mice from the cross of gray runner with albino waltzer to an animal recessive for both of these genes. From such a cross all four types of offspring are produced *in equal numbers:*

Gray runner (hybrid) female X albino waltzer male

produces

¼ gray runner ¼ gray waltzer ¼ albino runner ¼ albino waltzer

Here it has to be assumed that the gray normal hybrid forms four types of eggs:

gray runner .....(G R)*
gray waltzer .....(G r)
albino runner .....(g R)
albino waltzer .....(g r)

The albino waltzers breed true, and, therefore, appear to form only one type of sperm; each must have the genes for albino and for waltzing (g r). Thus from the equality of all four combinations among the offspring of the hybrid is inferred the equality of all four types of gametes, and from this it is assumed that the genes responsible are distributed to the gametes quite independently of each other. This means that it is purely a matter of chance whether the same egg which gets a "gray" gene gets a "running" or a "waltzing" gene. The *physical mechanism* which accounts for this independent assortment will be discussed in the next chapter. Just now it should be remembered that the assortment of the chromosomes to the gametes has been shown to be a chance affair, each pair assorting independently of every other pair.

Combinations and Ratios

It only remains to reconcile the equality among the different types of gametes produced by a "double hybrid" with the $\frac{9}{16}$: $\frac{3}{16}$: $\frac{3}{16}$: $\frac{1}{16}$ ratio which is obtained in the offspring of such hybrids, where characters showing dominance are involved. To do this, one may, in a purely mechanical fashion, make all the possible combinations of the four types of gametes produced by each parent. In Figure 10 the genes are represented by letters, the gametes by circles, and the zygotes or offspring by squares in the checkerboard, which is simply a device for making all possible sorts of gene combinations. As is obvious in the diagram, there are, out of each sixteen individuals, nine combinations with both dominant genes, three each with one dominant and one recessive, and one with two recessives.

This ratio is obtained time and time again wherever a cross involving two independent characters showing dominance is

* It has become the practice to represent genes by letters, capital letters standing for dominant genes and small letters for recessive ones. In the present case G stands for gray; g, for not gray—albino; R, for running gait; r, for waltzing.

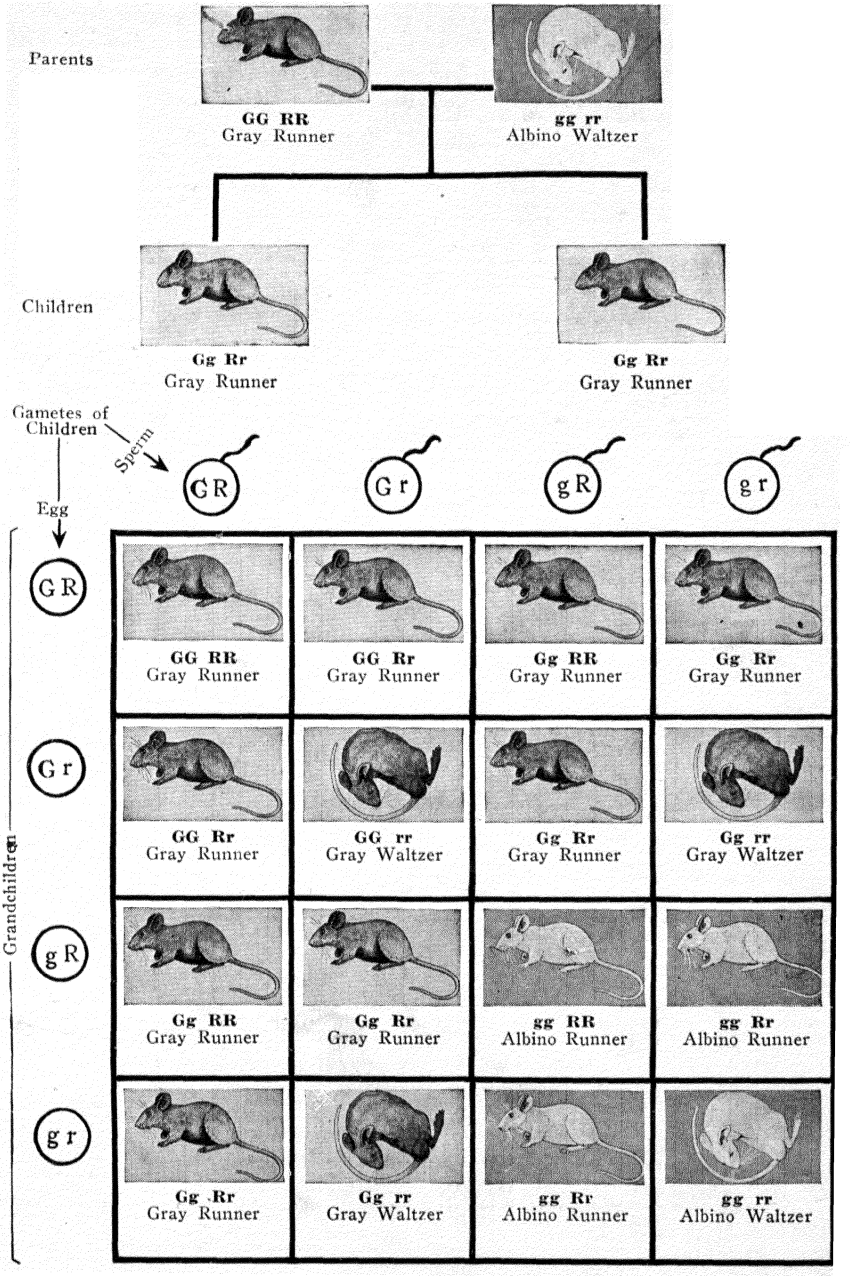


Fig. 10—INHERITANCE OF THE WALTZING HABIT AND OF ALBINISM IN MICE

Showing how the genes are distributed to the gametes and how the 9:3:3:1 ratio is produced

From a drawing by Mabel B. Little

followed into the second generation, and the conclusion is *that the two pairs of genes involved are transmitted in inheritance in complete independence of each other.*

Most people are prepared for some such conclusion as this, for they have heard many times: "The baby has his mother's eyes, his father's nose, and his uncle's bad temper." Our traits are obviously derived, some from one ancestor, some from another, and it is because they depend on separable units that they can be thus bandied about without losing their individuality. One of the chief reasons for the uniqueness of the new baby is that he does combine traits which had not before been combined. Many of the variations in men, in animals, and in plants are thus to be traced to new combinations of old units. Sometimes an old combination reappears, as for example, when the wild ancestral form appears in the progeny of domesticated animals. Such

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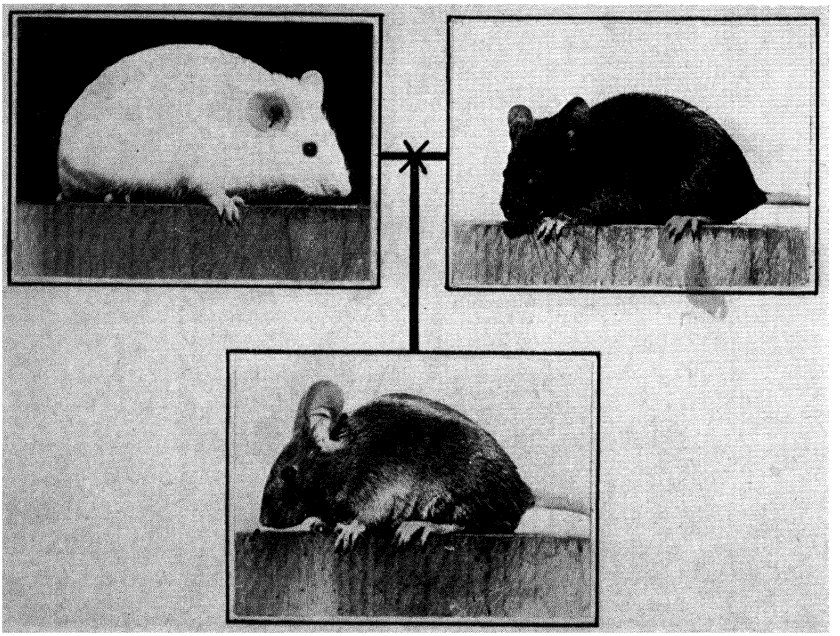

Fig. 11—"REVERSION TO TYPE"

The albino mouse (upper left) mated with the black one (upper right) produced only gray offspring (below) like the wild mouse. This was due merely to recombination of a gene for color (from the black) with a gene for the wild-type pattern carried but not shown by the albino parent

(*After Keeler*)

"reversions to type" used to be thought mysterious and many superstitions clustered about them. Now they may be produced in the laboratory and receive as simple an explanation as the following. An albino mouse crossed with a black one produces all gray offspring, a complete reversion to the wild coat color. These grays, however, when bred together, produce gray, black, and albino young in a ratio which indicates that grayness here depends on two genes, one of which is contributed by the black and one by the albino parent. The new variety gray is merely a new appearance of an old combination.

The number of possible character combinations increases much more rapidly than the number of gene differences. Thus, for two pairs of genes there are (with dominance) four (2^2) combinations—as in the case of color and waltzing in the mouse. For three pairs of unit differences there are eight (2^3) combinations; but for as few as ten gene differences there are 1024 (2^{10}) visibly different combinations of characters. If there were no dominance the last figure would become 59,049 (3^{10}). Experience indicates that the number of gene differences involved in any mating in man must in general be much greater than ten. Is it any wonder that there appear to be no duplicates among the children of men?

"Blending" Inheritance

Many persons will admit the reasonableness of the explanations advanced for the sharp segregation of certain hereditary characters in animals and plants, but they will frequently object that this is not the sort of inheritance which is encountered in common experience. They may have in mind observations on the appearance of their own children as compared with their parents. For example, if the parents differ greatly in height the children may vary between the parental extremes, or they may be even shorter or taller, or heavier or lighter than either parent. Variation in such cases seems to be continuous or intergrading, rather than sharp and discontinuous as in the case of color in fowls or mice or height in pea plants. How, they ask, can such cases be made to square with the ideas of genes which affect sharply contrasted, alternative conditions? The objection is valid and there is no doubt that many, perhaps most, of

the characters of animals, plants, and man do behave in this way. For years such cases of so-called "blending" inheritance seemed to be in a different category from the qualitative, sharply segregating characters to which Mendel's principles had been applied.

When some of these apparently non-conforming cases were examined in detail and the same quantitative experimental methods which Mendel had devised were applied to them, it was found that inheritance in these cases did not differ at all in principle from those studied by Mendel, but only in the *number* of genes involved. The clue was obtained when varieties of wheat differing in the color of their seeds were crossed. A red-grained wheat crossed with a white-grained race produced in the first generation plants with light red seeds and in the second generation a considerable array of grain colors from red through lighter shades to white. When the second generation plants were counted it was found that about 1/16 of them were as red as the red parent and subsequently bred true; about 1/16 were white and also bred true, and the rest were of intermediate colors. We have already seen that two pairs of genes reappear in a pure condition (*i.e.*, both members of the pair alike) in about 1/16 of the progeny of double hybrids, and it was only a logical step to assume that full red color depended on two rather than on one pair of genes.

In another cross the grandparental types reappeared in only 1/64 of the second generation, whereas the rest varied in color through all the intermediate conditions. If one has patience he may work out for himself the proportion of cases in which three independent pairs of genes appear in pure condition when triple hybrids are crossed. The answer is 1/64 and the conclusion is that here three pairs of genes are required to produce the full effect, and when only one or two genes are present only part of the effect is obtained.

The similarity between these cases and the usual experience of stockmen who cross animals or plants differing in size, yield, growth, etc., is striking. In such crosses the first generation is frequently intermediate between the parents, but the second generation is extremely variable, including only a few individuals out of large numbers which resemble the grandparents in the

characteristic considered. This variability is due to segregation of units in different combinations. The chief differences from the sharply alternative inheritance in the simpler cases first cited are: (1) The number of genes affecting these quantitative or blending characters is much greater; (2) These genes all affect the same character, such as size, in the same way, and usually do not show dominance.

Human Character Differences

The great variability of most human populations is probably due to the multiplicity of factors upon which most human traits depend, and since exogamy (marriage of unrelated persons) is the rule throughout civilized societies, new hybrids are continually being produced and segregation of many genes is continually occurring.

In man it is also difficult to determine just which traits are alternative to each other, since test crosses involving apparently single pairs of traits cannot be made. One of the greatest innovations in the whole study of inheritance was to separate the individual into single aspects and to determine which traits are alternative and therefore depend on a single pair of genes. Such information can be obtained for the human family only by carefully describing the parents and offspring over a number of generations and by constructing pedigree charts and family histories from which the inheritance of specific characters can be deduced.

This work has already progressed far enough to make it abundantly evident that simple alternative traits in man follow exactly the same rules of segregation and independent assortment which obtain in other animals and in plants. Such peculiarities as eye color (dark as contrasted with blue eyes), hair form (curly or straight), finger length (brachydactyly), right- or left-handedness, bleeder's disease (hemophilia), deafness, certain characteristics of the blood, and many other traits appear to depend chiefly on single genes. It has also become increasingly evident that many human differences are influenced by very many genes and that these are seldom found in pure condition. This is especially true of racial differences, which seldom show simple alternative segregation. In Negro-White crosses, for

example, skin color also behaves in inheritance very much like red grain color in wheat, depending on several independent pairs of genes which do not show dominance.

There is yet another way in which the Mendelian theory of heredity has often not satisfied the demands arising from common experience. The biologist who has demonstrated the operation of these laws in the inheritance of color and other more or less ornamental characters of fowls or guinea pigs or peas will often be given a polite hearing and will then be greeted with the remark, "Mendelism may be all very well as applied to these superficial traits, but does it mean anything more than this? Do the genes affect those deep-seated and fundamental characters on which the well-being and the very life of the animal depend?" Perhaps the best reply which the student of heredity can give is to point to the wealth of recorded experience which indicates that these principles apply to *all* characteristics of *all* organisms, but if he is wise he will quote chapter and book describing in detail actual cases showing how the genes effect differences of life-and-death importance.

Genes which Kill

In mice, for example, several genes are known which, when pure (both members of the pair alike), actually kill the

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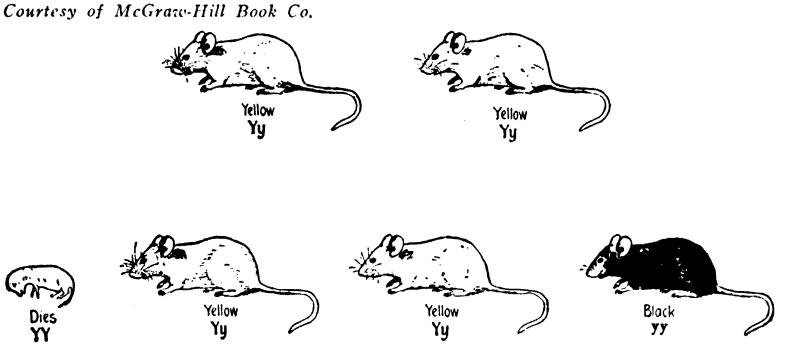
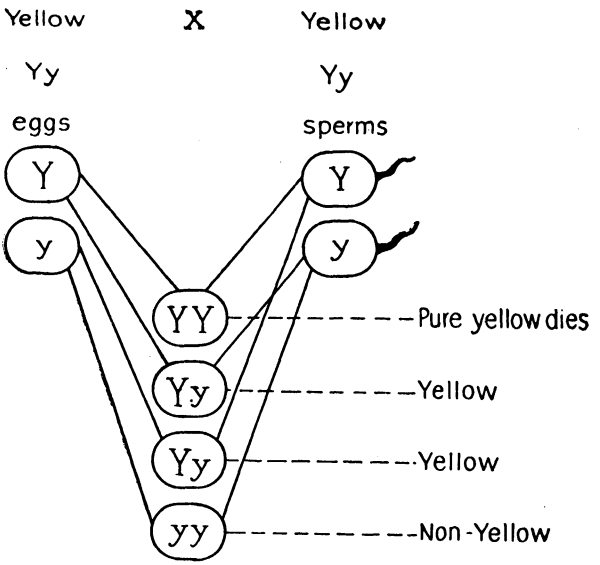


Fig. 12—INHERITANCE OF A GENE WHICH KILLS

A mating of a yellow mouse with a yellow mouse gives one-fourth dead embryos, one-half yellow mice, and one-fourth non-yellow ones

animal. The first case discovered was that of the peculiar yellow mouse, which always produces some black or gray young, as well

as yellows. No pure-breeding yellow mouse has ever been found. Experiments have shown that matings of yellow with yellow produce on the average about two-thirds yellow and one-third non-yellow offspring, but such litters are about 25 percent smaller than normal. The guess was made that the 25 percent of pure yellows, which should result from the mating of two hybrids, dies before birth, so that the results of such a cross could be symbolized as follows:



This was confirmed by the discovery of some 25 percent of dead and disintegrating embryos within the pregnant mothers (Fig. 12).

Many such genes are now known. They are called *lethal genes,* since they kill the new individual. They are probably not different in nature from other genes. It happens only that their effect on some vital structure or process is greater than the organism can survive. It is probable that the segregation of lethal genes accounts for some of the prenatal mortality which occurs in animals and man. They are an effective refutation of the criticism that "Mendelian" factors do not affect the vital processes.

Then there is the newly discovered case of the dwarf mice. Among the offspring of certain fancy mice were noticed some which stopped growing when about two weeks old. Their brothers and sisters matured normally, but the dwarfs, although healthy, never grew to be more than a third of the normal size and remained sterile. The dwarfs always made up about 25 percent of the litters in which they appeared. It is known that dwarfism acts as a simple recessive to normal size. In studying the dwarf it was discovered that a tiny gland at the base of the brain—the pituitary—was defective, and so into dwarfs were implanted pituitary glands from rats. The treated dwarfs now grew to normal size and the males became fertile, but the untreated ones remained sterile dwarfs. Here the "character" is not the color, nor the size of a minor part, but the whole development of the animal; it is affected radically by a single gene; and the gene exerts its effect on the body through a ductless gland, which in turn acts through the blood stream as a general coordinator of growth and sexual development.

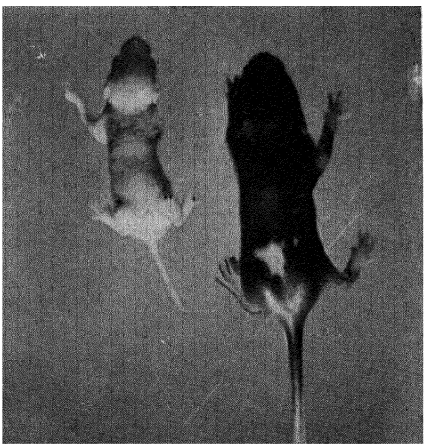


Fig. 13—SEGREGATION OF A LETHAL GENE IN MICE

These two mice are brothers, seven days old. The one on the left has an hereditary anemia (deficiency of red blood cells); the one on the right is normal. The difference is due to a single gene and, since this gene acts as a lethal or killing gene, all such anemic mice die soon after birth

The Gene and the Individual

Throughout this somewhat technical discussion there has been much talk of genes or factors as though all that mattered in a mouse or a man is the kind of genes which are parcelled out to him through the egg and sperm cells from which he takes his origin. In one sense this is true, for the nature of those single cells determines many of the fundamental characteristics which he will develop. If the egg and the sperm which unite to produce the embryo mouse each contain a gene for yellow, the fate

of that individual is sealed—it will die before birth. Likewise in man, if the uniting egg and sperm each contain a gene for blue eyes, one trait, at least, of that individual is settled.

We may, therefore, as a logical extension of the concept of the gene, conceive of the individual as an association of a large number of discrete separable units, each affecting some part of the structure and functioning of his body in a specific way. This view is defensible, because it accords with the experience we have of the way in which the visible characters of the parents are dealt out and distributed through the germ cells to the offspring. The characters of the individual behave as though they were separable. The individual, therefore, seems to be a kind of mosaic, a temporary aggregation of units, assembled for his lifetime, but shortly to be dissipated among his successors.

Courtesy of Harvard University Press

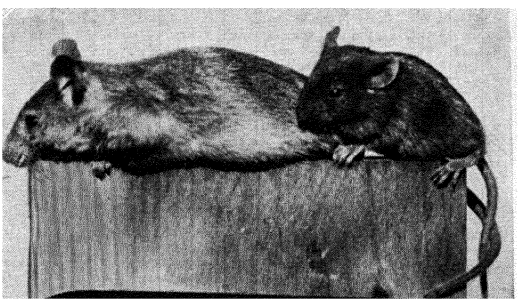


Fig. 14—A NORMAL AND A DWARF MOUSE OF THE SAME AGE

This difference is hereditary, but the deficiency of the dwarf may be made good by treatment with normal pituitary glands

(*After Keeler*)

Like many other general ideas about living things, however, this view is only one way of looking at a complex problem. In establishing the reality of the units on which heredity depends, it exaggerates their separateness and independence; for every living individual not only consists of an aggregation of structural units—genes, chromosomes, cells, tissues—but most remarkable fact of all, these units work together to produce one harmonious whole. Moreover, as we shall see, the genes act only within the limits of their environment. A child may inherit genes which, *if opportunity is provided,* would make him a musical genius, yet it is idle to expect a potential Mozart, born in an environment devoid of musical instruments, to become a great composer for the piano. All experience, both scientific and practical, shows that what is transmitted through the gametes is the capacity to react in specific ways to specific environment. The sum

total of the factors influencing the living substance—food, temperature, light, and the like—set the stage. The genes condition the internal or inherent end of the chain of action and interaction which produces the character of the individual. Before we can profitably discuss the relationships of the genes to the individual as a whole and to his environment we must understand something about their relationships to each other and about the mechanism by which they are carried from generation to generation and by which they build the vital fabric of the individual.

CHAPTER IV

THE MECHANISM OF HEREDITY

Questions to Be Solved

The idea that hereditary resemblances and differences depend on hypothetical units which are shuffled and dealt out to the offspring according to the rules of chance does not exhaust our interest in heredity. It only serves to whet our curiosity. What are these units? Where are they? How do they arise? Is their passage from one generation to another guided only by the two simple rules of segregation and independent assortment which Mendel proposed? Finally, how can answers to these questions "explain" heredity and the continuity and change which mark all life? These questions have been intensively studied since 1900, and the answers have begun to take form.

This new process of discovery has been fraught with continuous surprise and excitement, which has kept it in the center of the biological stage. It has led into the depths of the cell, and to the discovery of laws governing the behavior of its minutest parts; it has discovered glaring exceptions which threatened at one time to upset Mendel's principles entirely; and yet it has ended by extending, qualifying, and finally by establishing the underlying principles more firmly than ever.

The Methods Employed

This inquiry has involved two novel methods: (1) the intensive microscopic study of the cell, especially of the reproductive cells, which has gone hand in hand with (2) the detailed analysis through long continued breeding experiments of the hereditary constitution of a few animals and plants. We shall ask first what the microscope shows, and second, how this picture of the minute machinery of heredity coincides with that depicted by the experimental breeder.

By means of the compound microscope we are now able to magnify the structures found in material from animals and plants some two to three thousand times. Things almost incredibly minute thereby take on a reality as definite as that reported by the unaided sense. The cell, although it may be

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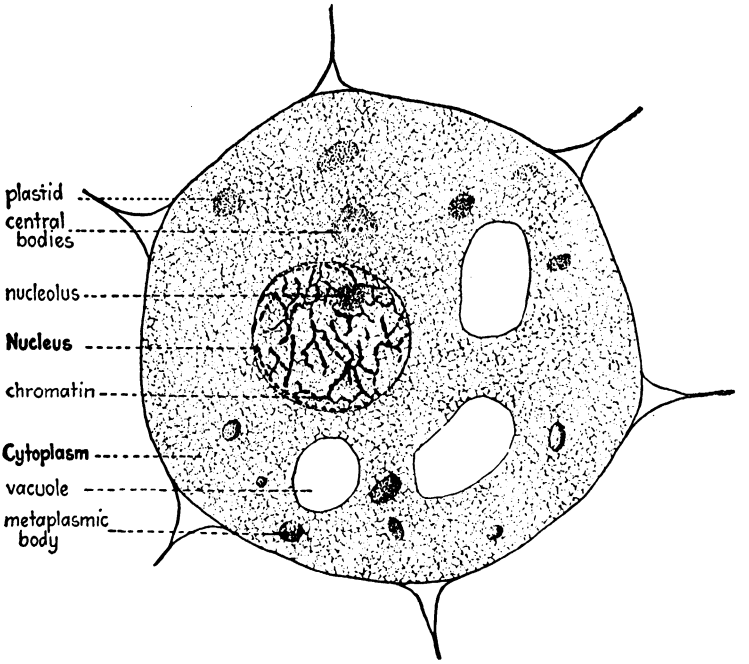


Fig. 15—DIAGRAM OF A TYPICAL CELL HIGHLY MAGNIFIED

measured in thousandths of an inch, to a cytologist seems now a gross structure; his interest has shifted to the smaller parts within the cells. We shall give the microscopist's report of the gross appearance of the cell and then follow him into the intricacies of its contents.

A typical cell is shown in Figure 15. Every cell contains a *nucleus* of denser material, surrounded by less dense *cytoplasm,* in which occur various structures with more or less constancy depending on the function and position of the cell. The nuclei of all cells contain a characteristic substance known as *chromatin* which is arranged in a definite pattern. This pattern appears when the nucleus divides, and is evident, first, in the number and

peculiarities of the very definite structures, the *chromosomes,* into which the chromatin always organizes itself, and secondly,

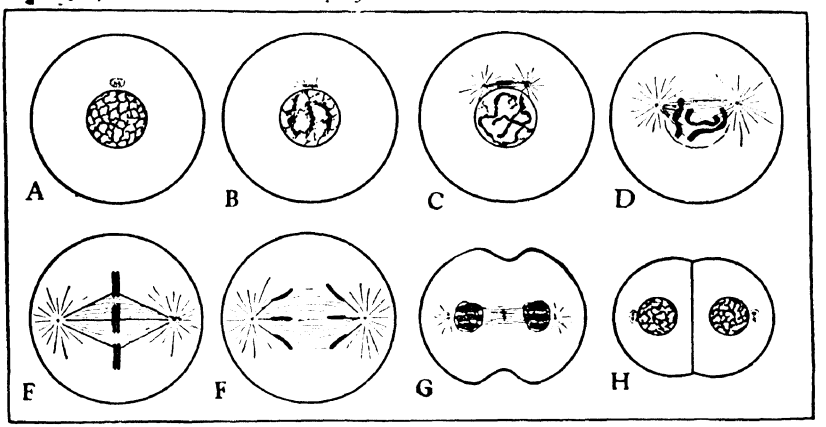


Fig. 16—HOW THE CELL DIVIDES
(After Sharp)

in the specific arrangement of the elements of heredity, the genes, within the chromosome.

Cell Division

All cells arise only by division of antecedent cells. Cell division is thus the basis of the continuity of life and upon it depends the transmission of life from cell to cell. This process is one of the most precise in the whole domain of biology. Essentially it consists in the exact duplication of each part of the nucleus of the cell and the distribution of the duplicate halves into the two daughter cells.

The duplication and distribution of the parts of the nucleus take place according to a complex series of steps which are essentially the same for all active cells. When the cell is about to divide, the chromatin of the nucleus, which, in the non-dividing cells appears as a scattered mass of granules (Fig. 16A), forms itself into a long coiled thread (Fig. 16B). This thread breaks into long, thin filaments, the *chromosomes,* the number of which is constant for all the cells of any species (Fig. 16C). In man, forty-eight chromosomes appear at each cell division; in the crayfish there are two hundred, in the pea fourteen, in the corn plant

twenty, etc. In bisexual animals and plants the chromosomes always occur in pairs. Thus in man the forty-eight chromosomes consist of twenty-four different pairs and the members of each pair are alike in shape and in all structural details (Fig. 17).

At this stage these long filamentous chromosomes may be observed to split longitudinally into two exactly equal halves (Fig. 16D). This is the essential feature of cell division and of reproduction, for every part of each chromosome seems to reproduce itself and to divide into two equal parts. The chromosomes then become shorter and thicker, the membrane about the nucleus disappears, and all the chromosomes, now doubled in number, arrange themselves in a double row across the equator of the nucleus (Fig. 16E).

Fig. 17—HUMAN CHROMOSOMES

Left, Spermatogonial plate of 48 chromosomes; *right*, anaphase of primary spermatocyte with the XY-chromosomes and three other chromosomes not yet divided—note evidences of splitting for next division

Drawn with camera lucida from human testicular material fixed in Bouin's fluid and stained with iron haematoxylin; magnification, 3600 diameters. Reprinted from *The Chromosomes in Man*, by permission of the authors, Herbert M. Evans and Olive Swezy

A most remarkable thing now happens. All the chromosomes on one side of the equator, containing one separated half of each chromosome of the parent cell, move as if drawn by a magnet toward a focal point at some distance from the equator; whereas all the chromosomes on the other side of the equator, representing the reciprocal halves of the original chromosomes, move toward another pole directly opposite to the first one (Fig. 16F). When each group of chromosomes has reached its goal,

a wall is formed across the whole cell, dividing the cytoplasm into two parts, each with its own chromosome group. The chromosomes at the same time disarrange themselves into the irregular network of granules, a nuclear membrane reforms, and the daughter cells resume their normal activities (Fig. 16G and H).

The Result and Significance of Cell Division

The result of this process is two cells where before there was one, and each, as far as its nucleus is concerned, is an exact duplicate of the other. This orderly, drill-like behavior of the chromosomes occurs each time a cell divides, and it is one of the wonders of life to observe how out of an apparently disorganized mass of chromatin, the chromosomes emerge at each division, always the same in number, in shape, and in character, only to disappear again into a resting nucleus.

The significance of these evolutions has only recently been realized in its entirety, for it is now known that the chromosomes are the bearers of those units of protoplasm, the genes, which determine the characteristics of the cell and consequently of the animal or plant. The genes behave as though they were ultramicroscopic parts of the chromosomes arranged in a line like beads on a string. At cell division it has to be assumed that each gene divides into two, and that each daughter cell receives an exact duplicate of each gene present in the chromosomes of the parent cell.

All animals and plants which consist of more than one cell grow by successive cell divisions of the sort outlined above. For many unicellular organisms it is likewise the chief means of reproduction, since after cell division in such forms the two daughter cells, replicas of each other, may break apart and each may form a separate individual. In some other organisms, a whole group of cells may break away from the parent body and set up in life as a new individual. These methods of reproduction by *fission* or *budding* or *fragmentation* are known collectively as *asexual reproduction.*

Most animals and plants, however, reproduce by a sexual process in which each parent contributes a single cell to the offspring. The preparation of the sexual cells—the gametes (egg

and sperm)—introduces an important variant of the process of cell division, the discovery of which was one of the essential steps leading to the present theory of heredity.

The Nature of the Gametes

In animals the male gametes, or sperm cells, are formed by the divisions of the cells of the *testis,* or male reproductive organ. Generally they are extremely small, and provided with some means of locomotion by which they are enabled to reach the larger and more passive female gamete, or egg. The eggs of animals are formed by division of the cells of the *ovary,* the female counterpart of the *testis.* They are larger than the sperms because they usually contain some stored food material, but even in birds, where the stored food in the egg may reach considerable dimensions, the egg, like the sperm, is a single cell with a single microscopic nucleus.

In animals generally the nuclei of the gametes are so extremely small as to be visible only with the higher powers of the microscope. All of the chromatin in the nuclei of the three thousand million germ cells from which the present human population of the globe arose would weigh only twenty milligrams, or about as much as a drop of water. We are not only asked to believe that all the hereditary characteristics of a man can be transmitted through such tiny bits of protoplasm, but we are, in fact, compelled to believe it by the evidence which follows and to acknowledge that a pattern of exquisite exactness exists within this microcosm.

Fig. 18 — CHROMOSOMES OF A PLANT DURING CELL-DIVISION

Showing Y-chromosome (upper center) going to one pollen cell nucleus and X-chromosome (lower center) to the other; magnified 1000 diameters

From a microphotograph by Karl Bělař

Gametes of Plants

In the higher plants the male gamete is a single cell contained within the pollen grain which is itself produced in the stamens of the flower; the female gamete, or egg, is produced within the ovule, a part of the pistil, the typically female part of the flower. When the pollen grain falls upon the pistil it germinates and sends into the female tissue a tube

which conveys the male gamete. This unites with the egg cell and by cell division gives rise to the embryo, or new individual, which is contained within the nutritive and protective structures of the *seed*. Here, likewise, two sexually different single cells are prepared and at fertilization fuse into a single cell from which the new individual arises.

Preparation of the Gametes

The processes which prepare the gametes are essentially similar in animals and plants, but are most easily illustrated by what occurs in animals (Fig. 19). In the testis previous to sexual maturity the cells multiply rapidly by ordinary cell division. Several of these cells, which are to form gametes, increase considerably in size, and then undergo a cell division

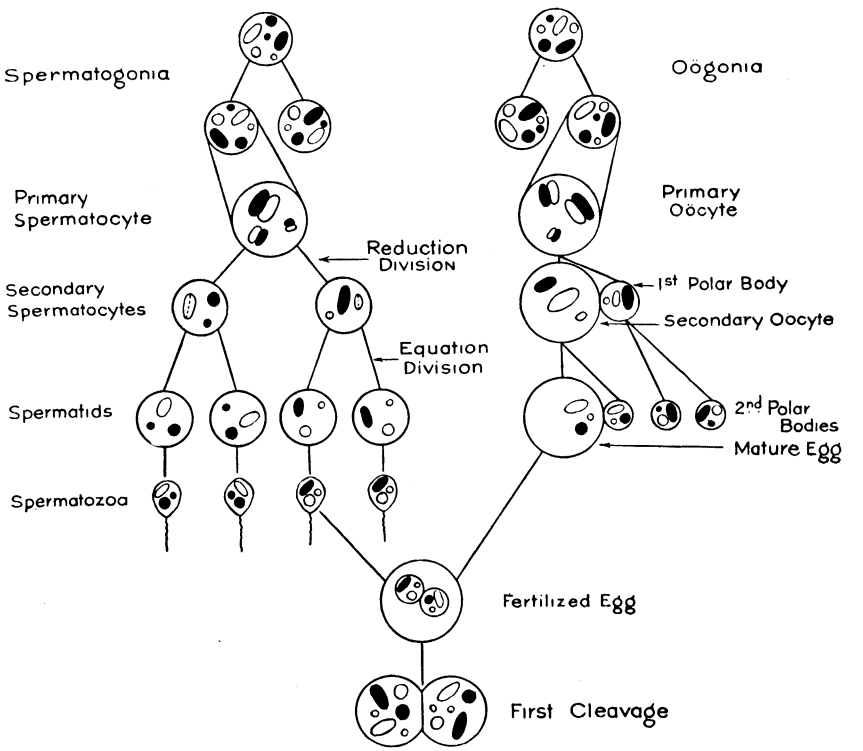


Fig. 19—PREPARATION OF THE GAMETES

From a drawing by Mabel B. Little

by which the number of chromosomes is reduced one-half. At this "reduction" division the chromosomes, *instead of splitting into two equal halves* as in an ordinary division, unite for a time in pairs at the equator of the nucleus, and then separate or disjoin. One member of each of these temporarily united pairs is drawn to each pole of the spindle, so that each daughter nucleus gets one member of each pair, and thus one-half of the total number in the parent cell.

The Cells and the Chromosomes

Thus in the formation of the human sperm, the cell destined to produce sperm, like all the body cells, has forty-eight chromosomes. These unite at the reduction division into twenty-four pairs and one member of each pair goes to each of the daughter cells, which consequently have twenty-four instead of forty-eight chromosomes. These twenty-four chromosome cells then divide by the splitting of each chromosome into two, so that from each original cell are produced four cells with twenty-four chromosomes. Upon the formation of the resting nucleus, and the addition of a tail and head-piece (Fig. 19), these become functional spermatozoa, consisting chiefly of nucleus with accessory structures, but almost no cytoplasm.

The events in the female are similar, except that at the reduction division two cells are produced, each with the halved number of chromosomes, although the cytoplasm does not divide, but is retained by the larger cell, which eventually becomes the functional egg. The small nucleus which has thus been extruded is the first polar body. Both the egg and the polar body now divide equationally. Again the cytoplasm is retained by the egg and the nucleus is extruded as a second non-functional polar body. Thus from the original cell are produced four cells with the halved number of chromosomes—a large egg with one nucleus and considerable cytoplasm and stored food for the future embryo and three small polar bodies which degenerate. At fertilization the sperm and egg nuclei unite to form the zygote, or individual, and restore the double, or diploid, number of chromosomes. All gametes are, therefore, haploid cells, *i.e.*, with the halved number of chromosomes, but all the cells of the zygote, or complete individual, are diploid.

The Pairs of Chromosomes

During this process the significance of the paired arrangement of the chromosomes becomes apparent, for it is now known that of the twenty-four pairs of chromosomes in man, for example, one member of each pair has come from the mother and one from the father. At the reduction division, the members of each pair unfailingly seek out each other and unite temporarily. When the pairs separate, each member goes to one of the two resulting cells, but it is entirely a matter of chance to which of the two cells any single member of a pair is drawn. Thus one gamete may get twenty chromosomes which came from the father and only four which came from the mother, or any other combination, provided always that each gamete gets *one representative of each pair of parental chromosomes.* The gametes are thus truly representative cells containing samples, equal in number, but not all alike in respect to origin, of all the chromosomes of the parent.

So much—and much more—the microscope shows. We now emerge into the common light of day and look once again at the grosser external characters of the organism. What can be learned from breeding experiments concerning this intricate mechanism of heredity?

The Fly "Drosophila"

By far the greater part of our knowledge in this respect was first obtained from one small fly—*Drosophila melanogaster,* the vinegar or pomace fly—concerning whose life and heredity more complete knowledge is available than for any other living creature (Fig. 20).

It has been said that Drosophila seems to have been made to order for the study of heredity. It lives on easily prepared food in small bottles and reproduces with great rapidity and in enormous numbers. It is probable that some thirty million of these tiny insects have been bred experimentally under close observation. A generation is produced every twelve to fourteen days, an average of about twenty-five generations a year, or some five hundred generations in twenty years. When we consider that it takes about 15,000 years to produce 500 genera-

tions of men, it is not surprising that we have learned more about the hereditary machinery of Drosophila than we have about that of men directly.

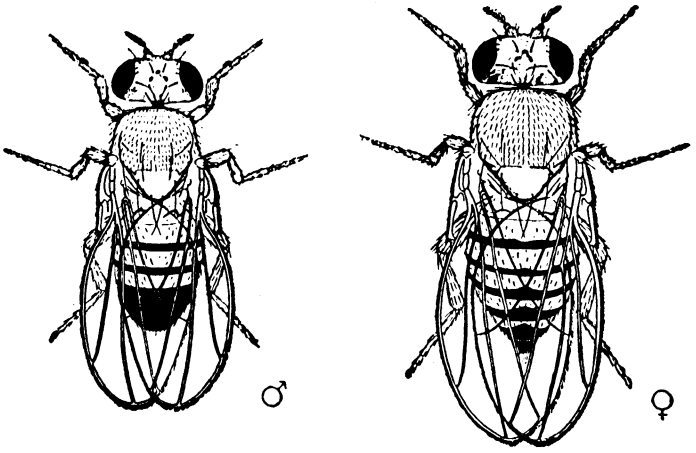


Fig. 20—MALE AND FEMALE DROSOPHILA
(*After Morgan*)

Moreover, because of the enormous numbers of individuals and generations observed, more hereditary differences have been found in Drosophila than in any other animal or plant. Over 500 individual genes have been studied, affecting every conceivable aspect of the organism. For these reasons Drosophila has now been drawn from its modest retirement in fruit shops and cider mills and has become a public character.

Although Drosophila has occupied the center of the stage, it has not been the sole actor in the play. During the years since the "rediscovery" of Mendel's principles, hordes of animals and of plants have been bred in laboratories, greenhouses, and fields over the whole world, and the chief discoveries on one species have been extended and verified on many, so that there is little chance that the sudden expansion of our knowledge of heredity has been merely a flash in the pan, or is to be ascribed only to the idiosyncrasies of a few animals and plants.

The Genes and the Chromosomes

The essential result of this labor has been the emergence of new principles describing the location of the genes in the repro-

ductive cells, and the physical mechanism which underlies their orderly distributions. Like Mendel's principles, these new laws were first derived from the statistical results of breeding experiments, but unlike Mendel's, they have been continually checked by reference to the physical mechanism in the cell.

Such a mechanism for heredity had long been suspected. The finger of suspicion had pointed especially at the chromosomes of the gametes as the bearers of the heritage which the parents passed on to their progeny. Here were structures which in many ways behaved just as the genes did. Both chromosomes and genes behave as individual units; both occur in the animal and plant body cells in pairs, the chromosomes as visibly paired rods; both receive one member of their respective pairs from the father and one from the mother; both chromosomes and genes *segregate* when the gametes are formed, one member of each pair going to each gamete, which thus contains half the

Fig. 21—WHERE DROSOPHILA ARE BRED BY THE THOUSANDS

Each half-pint milk bottle on this student's desk is the home of 200 to 500 small flies. To observe the results of breeding experiments the flies are etherized and poured out on white plate where their characters may be observed and the number counted under the binocular microscope

number of chromosomes and one representative of each pair of genes.

There was a reasonable assumption that the genes were carried in the chromosomes, but this would have remained mere assumption and the most interesting parts of the chromosome theory of heredity, *i.e.*, those concerned with the exact arrangement and behavior of the genes in the chromosomes, would have remained unknown, if proof from an unexpected source had not appeared. This was the observation that males and females were not quite identical as regards their chromosome pairs. In some animals an odd unpaired chromosome was found in the male. A male of such a species had, let us say, fifteen chromosomes, whereas the female had sixteen. Then, another exception to orthodox ideas appeared when one character was found in Drosophila which was not transmitted equally by the father and mother. This exception was discovered in the course of breeding experiments, and it was the starting point of the brilliant and sustained study which has given so complete a picture of the intricate machinery by which living things transmit their resemblances and their differences.

Dr. Morgan's Experiments

It happened that in 1910 Dr. T. H. Morgan, then of Columbia University, was breeding wild vinegar flies—Drosophila. The large compound eyes of the wild flies are red, but in one culture appeared a fly with white eyes. Mated with a wild red-eyed female all the offspring, as expected, had red eyes, and in the second generation three-quarters of the flies had red eyes and one-quarter had white eyes—but *all of the white-eyed flies were males* (Fig. 22).

In further breeding, white females appeared, and when these were crossed with pure red males a most unusual result was obtained in each case. The daughters of this cross always had *red* eyes, but the sons always had *white* ones (Fig. 23). It looked as though the *red* female transmitted a normal red gene to every offspring, whereas the red male transmitted a red gene only to his daughters. This is just what would happen if the female had an equal pair of chromosomes each bearing a gene for red, and if one member of this pair went into every egg; but

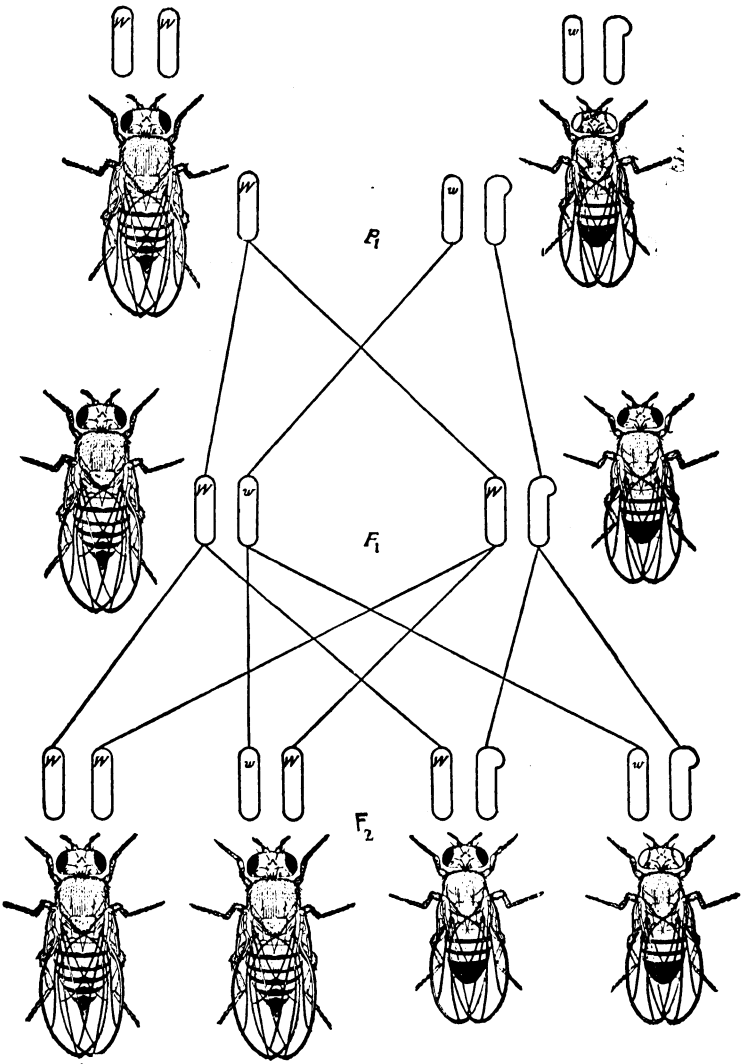


Fig. 22—SEX-LINKED INHERITANCE IN DROSOPHILA

Red-eyed female crossed with white-eyed male. The course of the sex-chromosomes carrying the sex-linked gene *W-w* is traced from parents to F_2. The hook-shaped (Y) chromosome of the male is not exactly equivalent to the sex chromosome and is shown as carrying no genes. Females at left, males at right. Reproduced from *Mechanism of Mendelian Heredity* by permission of the author, T. H. Morgan, and of the publishers, Henry Holt and Company

if the male had only one of these chromosomes, only half of his sperm could get it and thus get the gene for red that it carried.

The similarity to the cases in which an odd unpaired chromo-

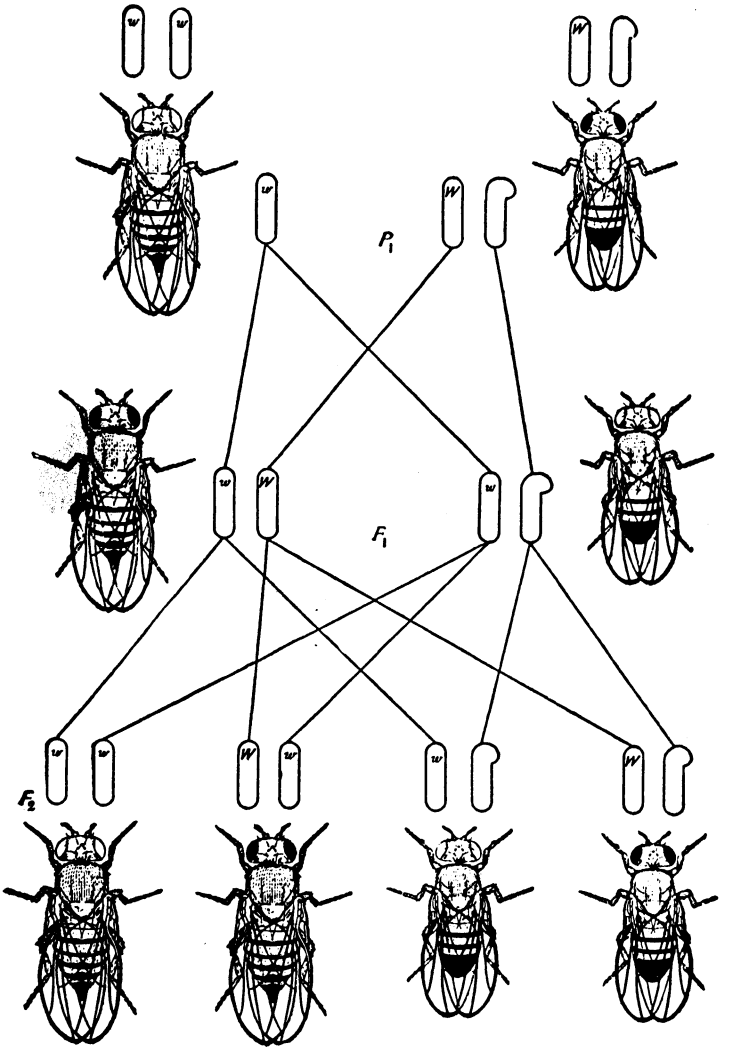


Fig. 23—SEX-LINKED INHERITANCE IN DROSOPHILA

White-eyed female crossed with red-eyed male. The reciprocal of the cross shown in Fig. 22. Females at the left, males at the right. Reproduced from *Mechanism of Mendelian Heredity* by permission of the author, T. H. Morgan, and of the publishers, Henry Holt and Company

some had been found in the male was noticed and the assumption made that in Drosophila the pair of genes for red or white eyes are located in this pair of chromosomes. This was then tested and proved, both by breeding experiments and by microscopic examination of the cells of males and female flies, and for the

first time a firm connection was established between a Mendelian gene and a single structure in the germ cells.

The chromosome which bore this gene was called the sex or X chromosome, because it appeared to be represented twice in females and only once in males*, and thus indicated or determined the actual difference between the sexes. The connection or linkage between this chromosome and the genes for red eyes and those for white eyes was called *sex-linkage,* and soon a whole series of characters which behaved in this way was discovered. These were always transmitted in the same peculiar criss-cross manner as white eyes; going from the father to his daughters. In man and other animals the same sort of inheritance has been discovered, and it rests not on any exception to the principle of segregation but on the peculiar circumstance that some genes are located in chromosomes which are distributed to all the gametes of one sex but to only half the gametes of the other sex. The discovery of this chromosome mechanism has now led to a theory of the way in which sex itself is determined, but this will be discussed later. Just now the important point is that certain of the factors of inheritance seem to be located in a definite chromosome.

From this beginning grew the general idea that all of the genes which determine the characters of the organism are located in the chromosomes; that each gene has a definite location in a specific chromosome and that the laws governing the distribution of the genes are actually the laws governing the distribution of the chromosomes and their parts to the germ cells. The proof of this conception of the architecture of the hereditary material is largely the work of Professor Morgan and of his associates, A. H. Sturtevant, C. B. Bridges, and H. J. Muller, aided by the students who came to their laboratory at Columbia.

Other Discoveries

The new principles were discovered as a result of the study of exceptions to the old laws. The English biologist, William

* In the male although only one X chromosome is found there is also another member of this pair, slightly different from the X in shape and known as the Y chromosome. This carries no genes and is transmitted from father to sons only as shown in Figures 22 and 23. See page 71.

Bateson, who was one of the first to appreciate and to extend the ideas of Mendel, had a habit of saying, "Treasure your exceptions." When nature does not behave in exact accordance with the laws deduced by men, it usually means that the laws are either wrong or incomplete, and recognition of this fact is usually the first step in new discovery. So it was in the case of heredity. Bateson himself noticed that when certain varieties of sweet peas which differed in flower color and pollen shape were crossed, the assortment of the two characters in the second generation did not take place at random, as required by Mendel's principle of independent assortment, but the parental combinations were too numerous and the new combinations too few, as though these genes had tended to stick together in inheritance instead of separating from each other when the gametes were formed.

As soon as the Drosophila experiments were well under way many exceptions of this kind were found and explained. A simple case is shown in the diagram (Fig. 24). A black long-winged fly crossed with a gray vestigial one (sex makes no difference here) produces all gray long-winged offspring. Black and vestigial are known to act as simple recessives to gray and long, so we should expect these hybrid flies to form gametes *BV* (gray long) and *Bv* (gray vestigial), *bV* (black long) and *bv* (black vestigial) in equal numbers. The easiest way to test the kinds of gametes formed is to cross such a hybrid with a doubly recessive one—*i.e.*, a black vestigial fly which forms only gametes *bv*. None of these gametes can introduce a dominant gene to hide the segregation of the genes from the hybrid, and so the progeny from the hybrid mated to the black vestigial fly should show the ratio in which the gametes of the hybrid are formed.

One cross like that shown in the diagram produced 3236 flies as follows:

Parental Combinations	gray vestigial : 1294 black long-winged : 1418	about 83%
New combinations	gray long-winged : 283 black vestigial : 241	about 17%

This does not agree at all with Mendel's second law, for the different types of gametes are not produced in equal numbers.

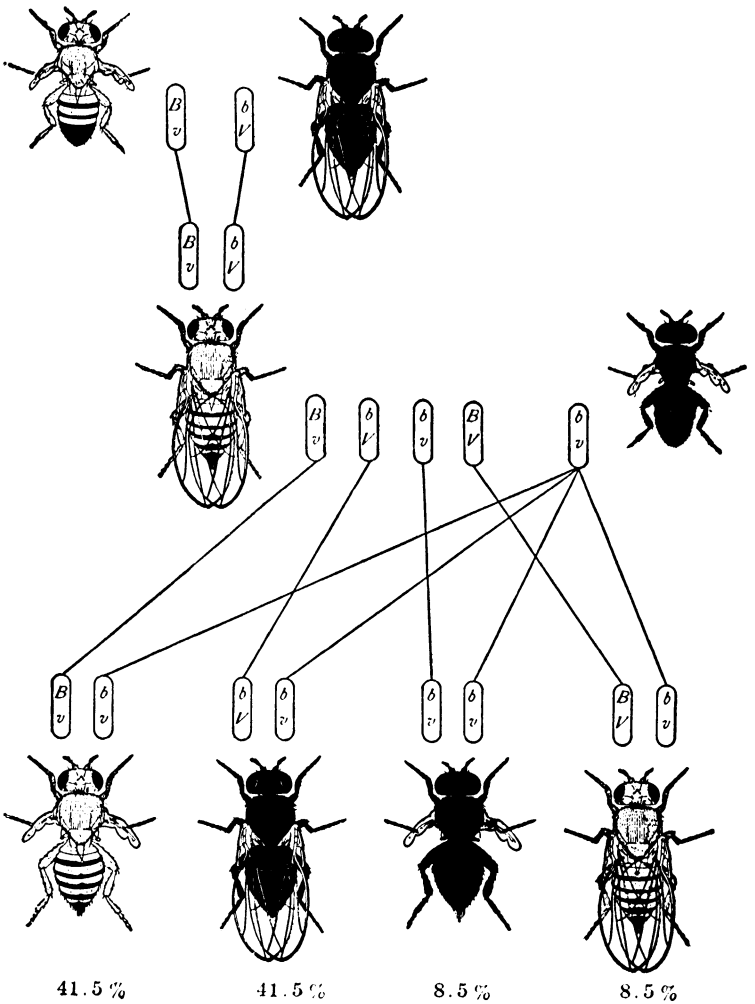


Fig. 24—LINKAGE IN DROSOPHILA

Results of a cross between a gray, vestigial male and a black, long female; and of a backcross of the F_1 female with a black vestigial male. Reproduced from *Mechanism of Mendelian Heredity* by permission of the author, T. H. Morgan, and of the publishers, Henry Holt and Company

Instead, there are too many of the combinations as they appeared in the parents; and too few of the new combinations. The genes for gray and vestigial and for black and long-winged have tended to stick together and to come out of the cross together more often than apart.

The Genes Stick Together

If we reverse the combinations in the parents, then the favored combinations in the progeny are reversed. Black vestigial flies crossed with gray long-winged flies produce again all gray long-winged progeny, and such hybrids crossed to black vestigial produce about 83 percent of *gray long-winged* and *black vestigial* flies (the parental combinations) and only 17 percent of *gray vestigial* and *black long-winged*—the new combinations. Here again the genes tend to stick together in their parental or original combinations. This tendency, which broke the second law of Mendel, Morgan called *linkage*. Certain genes seem to be linked together in heredity and do not segregate independently. It is typical of linkage, however, that it is seldom complete. Even linked genes do break apart to form new combinations and this breaking apart process was called "crossing-over"—for a reason shortly to be discussed.

In the course of the extensive experiments with Drosophila, four groups of linked genes were discovered. All of the genes in any one group tended to stick together with various strengths as measured by the proportion of the cases in which they broke apart. But all the genes in any one group showed independent assortment with the genes in the other groups.

Explaining Gene Associations

How, now, is this surprising association between the genes to be explained? What physical force holds linked genes together in inheritance? The results, said Morgan, are just those to be expected if linked genes are carried in the same chromosome, held together by the structural integrity of the chromosomes which pass as units into the gametes. If this were the case, all the genes in the same chromosomes should be linked together, but should show independent assortment with the genes in the other chromosomes. Thus Mendel's law of independent assortment would apply only to genes from different chromosomes.

Microscopic study showed four pairs of chromosomes in Drosophila (Fig. 25), and all the genes studied fell into four linkage groups. Moreover, one large group of linked genes

showed the peculiar criss-cross inheritance (the "white-eye" type), which indicated that they were located in the largest, or X, chromosome, known to be specially concerned with sex; two large groups of genes could be assigned to the two other large chromosomes; one linkage group contained only a few genes, and the fourth chromosome was very small. Finally, when it was shown that the absence or misbehavior of a certain chromosome as shown by the microscope meant the absence or parallel misbehavior of a certain group of genes, it became practically certain that the location of the factors of inheritance had been found.

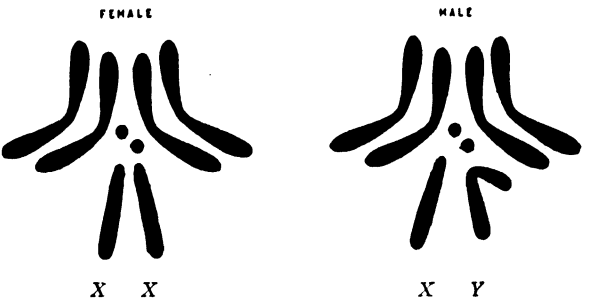


Fig. 25—THE FOUR PAIRS OF CHROMOSOMES IN DROSOPHILA

X and *Y* designate the sex chromosomes

(*After Bridges*)

The behavior of the chromosomes explained the behavior of the genes very nicely except in one particular. If two genes stick together in inheritance because they are in the same chromosome, why don't they always stick together? The fact is that they usually do not—they associate only in a majority of the cases. There must be some mechanism by which the association between two genes in the same chromosome can be broken. The mechanism which the Drosophila investigators imagined was that the two members of a pair of chromosomes might exchange parts and that the genes in these parts should thus "cross over" from one chromosome to its mate.

Cross-Overs or Breaks in the Linkage

At the union of the members of the pairs of chromosomes just before the gametes are formed, something resembling an exchange of parts is seen to take place. The members of each pair twist about and cross each other at one or more points, and if the chromosomes should break at these points, there would be just the opportunity for exchange of parts which the theory of

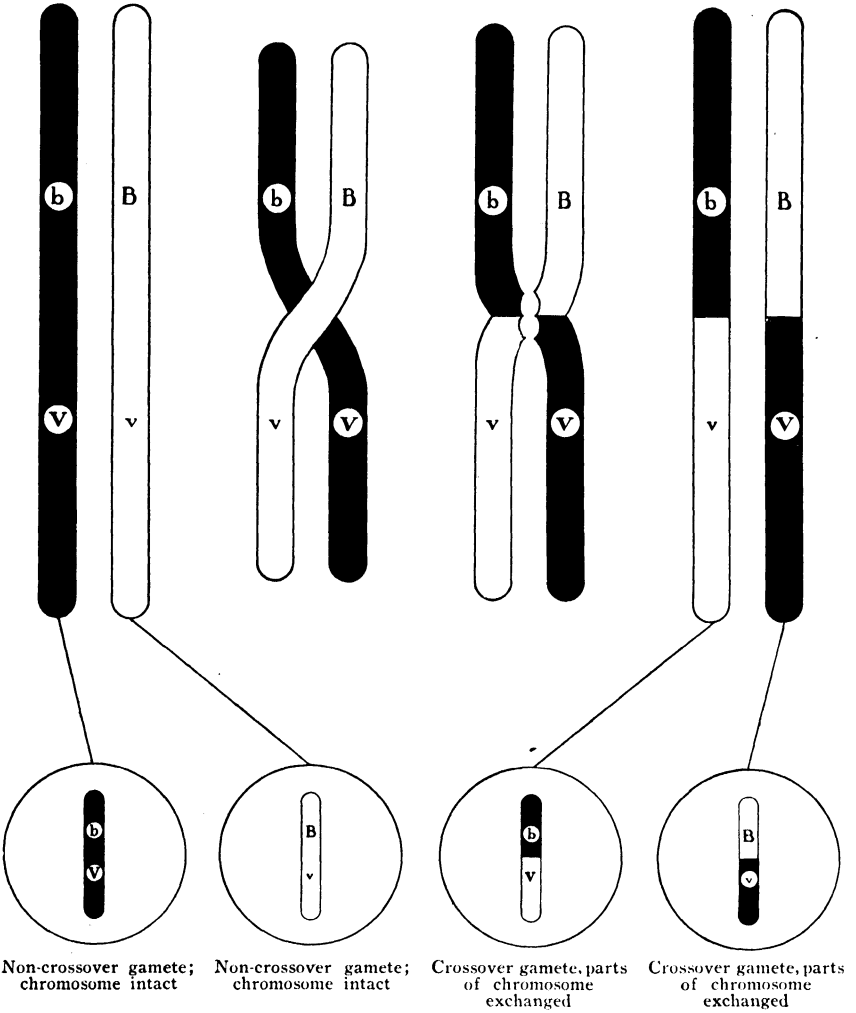


Fig. 26—HOW CROSSING OVER OCCURS
From a drawing by Mabel B. Little

crossing over demands. What takes place at this time is shown in Figure 26. This exchange of parts between members of a pair of chromosomes has been actually observed through the microscope by Dr. Curt Stern.

The crossing over or recombination of genes in the same chromosome pair was found to take place with a remarkable order and constancy. Thus each time that black bodied flies were crossed with vestigial winged ones the genes for black and for

vestigial tended to appear together (*i.e.,* to cross over) in 17 percent of the gametes of the hybrid; whenever vestigial winged flies were crossed with purple-eyed ones these genes "crossed over" and appeared together in 13 percent of the cases; while black and purple showed consistently about 6 percent of crossing over. The same two linked genes always showed the same percent of crossing over, and thus all the genes in any chromosome could be arranged in a consistent order according to the amount of crossing over which they showed with other genes in that group.

Now appeared one of the most ingenious ideas in the whole theory of heredity: the frequency of these cross-overs or breaks in the linkage *was assumed to depend on how far apart the genes are.*

If they are very close together in the chromosome they ought to stick together very tightly in inheritance; but if they are farther apart they ought to separate more frequently, merely because there is more likelihood of a break occurring in a long distance than in a short one. Thus if it could be shown that the genes were arranged in one line along the chromosome the distance between genes on this line could be measured by counting the relative number of times they broke apart or crossed over.

Mapping the Genes

To condense the result of an enormous amount of work into very few words this linear order of the genes was established, these distances were measured in this way for all available genes in Drosophila, and chromosome maps, showing the location and distances of the chief genes (about 300 of them) in all four chromosomes, have been made (Fig. 27). Distance in these maps does not correspond directly with cross-over values, but is proportional to them, an item in the technique of mapping which cannot be discussed here. The proof of the pudding is in the eating, and these maps of the Drosophila chromosomes actually work, for by their use the results of matings may be predicted with great accuracy. They provide the means for an almost uncanny control over the characteristics and the whole life of Drosophila. These animals may now be made up to order, somewhat as a prescription is filled, the forms and com-

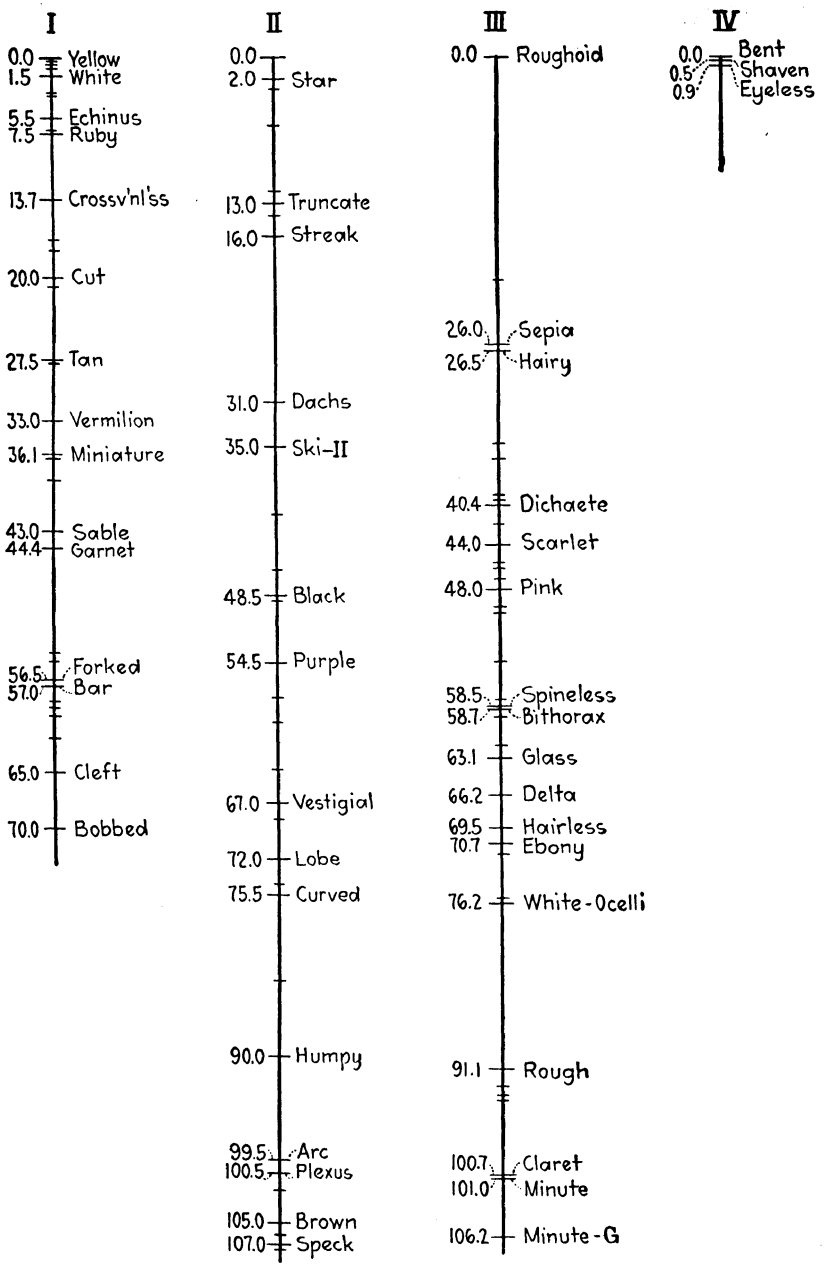


Fig. 27—THE "GENE-MAP" OF THE DROSOPHILA CHROMOSOMES

Showing the location of some of the more important genes

(*After Morgan, Bridges, and Sturtevant*)

binations of characters limited only by the kinds of genes available and the skill and knowledge of the manipulator.

Similar maps for several other animals and plants are now under construction. In one of our most valuable plants, maize, ten groups of linked genes, corresponding to the ten chromosomes have been identified; in several other species of Drosophila linkage groups corresponding to the number of chromosomes have been found; in the garden pea with seven chromosomes five groups have so far been discovered. Mendel himself, however, gave an unwitting demonstration that the number of independent genes corresponds with the number of chromosomes, for he studied seven pairs of genes and found them all to be independent. By a most unusual chance he happened to hit upon only one gene from each chromosome. Man with his twenty-four pairs of chromosomes is among the entirely unmapped animals and will probably remain so, for it is most difficult to locate genes in a large slow-breeding mammal which insists on choosing his mate for reasons which are not related at all to the solution of linkage problems.

This new kind of topography is startling and spectacular, but does it really make heredity and the underlying problems of life any more comprehensible? The biologist at least will insist that it does, because the mapping of the genes and the new principles of linkage and crossing over and chromosome location on which mapping rests are after all condensed expressions of what we know about heredity. Because they do summarize our experience they allow us to predict the outcome of specific crosses and in this sense to exercise some control over heredity. That ability in itself is always one of the best tests of improved understanding.

The Importance of the Gene

But the exact location of the genes in the chromosomes does more than that. It tells us that genes are real physical entities which obey physical laws. They tend more and more to lose the abstract character which Mendel gave them and to become actual flesh. Now we may think of them as actual parts within the chromatin material of the nucleus of every cell. Because of the large number of genes (several thousand in Drosophila) and the very small space into which they are packed (the total

volume of the Drosophila chromosomes in one nucleus is probably not much greater than .236 cubic microns),* they must be beyond the range of vision even of the ultra microscope and must be of the same order of size as some large organic molecules. It is doubtful if we shall ever see the gene, but by its behavior it seems to be a structure of such constancy and it obeys such reasonable laws that we really do not need to see it. By its work we know it.

A New Conception of Life

With the gene we reach a new conception of continuity and change in life. Our ideas of what it is that continues and of what it is that changes have undergone a progressive narrowing and refining. First we learned that living substance—protoplasm—was continuous; next that continuity depended on the division of the cells. Within the cell it was chromosomes whose exact division provided for chromosome continuity; and now within the chromosome we find the *lowest level of physical organization and continuity—the gene.*

The resemblance of parent and offspring depends at bottom on the reproduction of the genes of the parents and their passage into the germ cells. Changes, as we shall see in Chapter VI, arise when at some rare cell division a gene reproduces not another gene exactly like itself but one slightly different. The gene seems at present to be the smallest unit of continuity and change. We must be a little careful in referring to it as the "ultimate" unit of life, for the atom was thought to be the ultimate unit of matter until the electron proved to be "more" ultimate. History may repeat itself with the gene.

*A micron is about 1/25,000 of an inch.

CHAPTER V

HEREDITY AND SEX

The Problem of Sex

The same discoveries which revealed the physical mechanism of heredity threw a flood of new light into that dark corner where lurked the problems of sex. The popular mind had speculated more about this than about almost any other biological question, and the problem itself had been complicated and obscured by superstition and by contradictory theories resting frequently on incorrect and incompletely ascertained facts. The establishment of Mendel's theory of heredity and the investigation of the finer details of the process of reproduction greatly clarified the problem, and we shall here simplify it still further by trying to find an answer to one chief question which has plagued human curiosity for generations: How does it happen, in man and the higher animals, that of two individuals so alike in many ways one is born a male and another a female?

Is Sex Hereditary?

This question concerning sex is similar in many respects to that which may be asked about other traits in which individuals differ. In trying to find out what laws govern the transmission of likenesses and differences in such characteristics as color, form, size, and behavior, we found that the most fruitful questions to ask were how these traits were represented in the gametes, and how they were distributed to the offspring. Although in the higher animals sex seems to be a more fundamental and complex character than, for example, eye color, it now appears to be in the same category, and may be studied in much the same way. Sex is now known to be largely a matter of heredity, and the sex difference in most animals appears to be determined by the nature of the gametes which unite at fertilization.

The Sex Difference

Fundamentally, of course, sex is a method of reproduction involving always two unlike reproductive cells—egg and sperm.

Courtesy of the New York Zoological Society

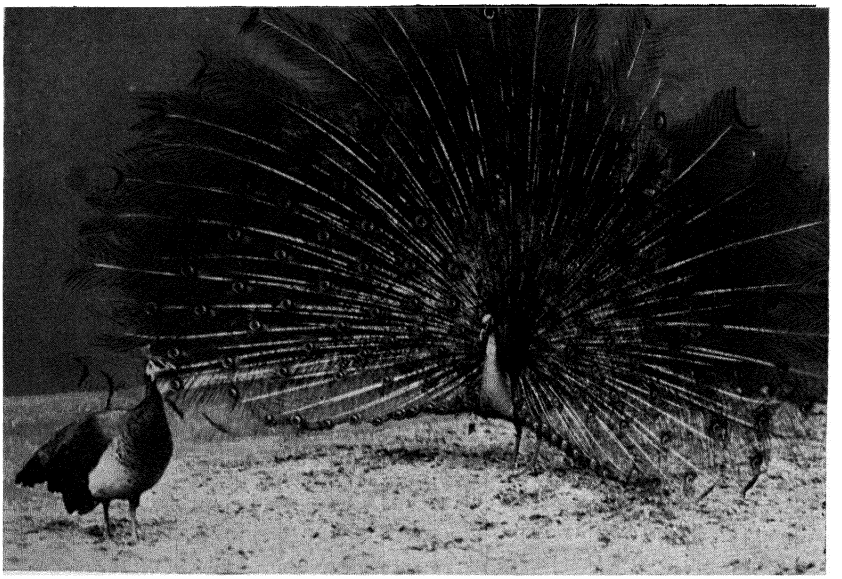
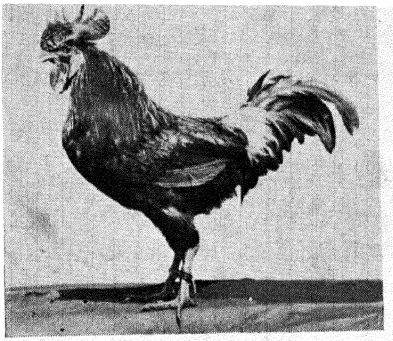
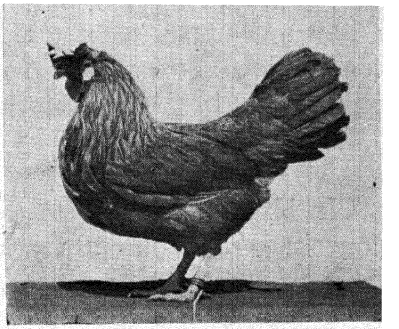


Fig. 28—PEACOCK AND PEAHEN
Showing sex difference in plummage

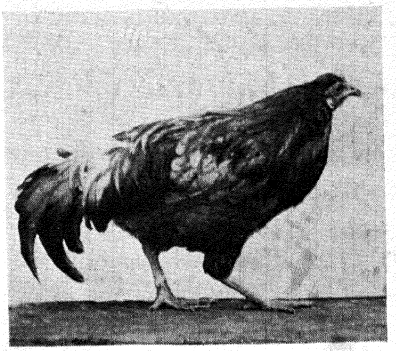
In the higher animals these cells are generally produced by different individuals, and we may briefly define a male as an individual which produces sperm and a female as one which produces eggs. This is the primary difference, but it imposes secondary differences in other structures, functions, and habits which are directly or indirectly concerned with reproduction; and the term sex in ordinary parlance includes these more evident characteristics. These differences in bi-sexual animals involve chiefly the type of reproductive gland, or *gonad,* and the secondary sexual features which are so often conditioned by the gonad. The male reproductive glands, or gonads, are known as *testes;* in these the sperm are produced by a peculiar series of cell divisions (see Chapter IV). Accompanying the testes are various accessory ducts and other organs by which the sperm are conveyed to the eggs. The distinctive female organ is the



NORMAL MALE

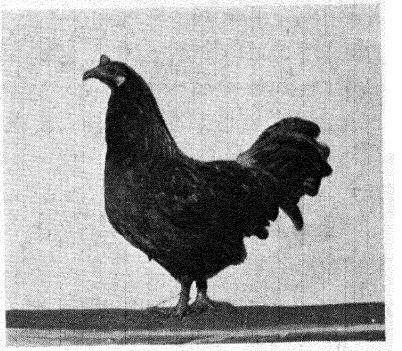


NORMAL FEMALE



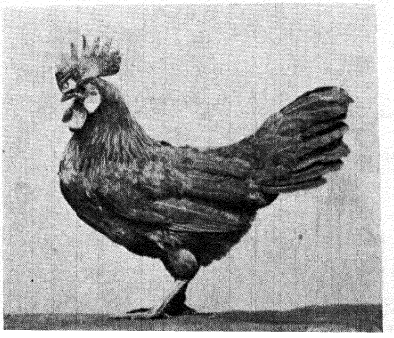
CASTRATED MALE (CAPON)

Male type body and plumage, undeveloped comb



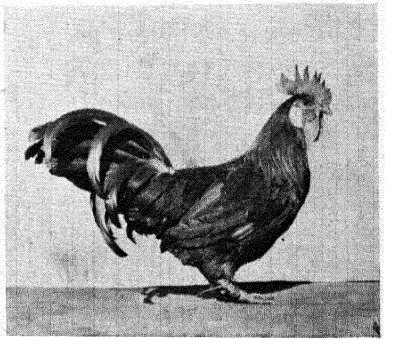
CASTRATED FEMALE (POULARDE)

Female type body, male plumage, undeveloped comb



A FEMALE INTO WHICH A TESTIS HAS BEEN GRAFTED

Female body-form and plumage, but male comb



CASTRATED FEMALE IN WHICH RIGHT OVARY (USUALLY RUDIMENTARY) HAS DEVELOPED AS A TESTIS

Male plumage, male coloration, male comb, but female type body

Fig. 29—BROWN LEGHORN FOWLS, SHOWING THE CONTROL WHICH THE GONADS EXERCISE ON THE SECONDARY SEX-CHARACTERS

Photographs from the experiments of Dr. Alan W. Greenwood, University of Edinburgh

ovary in which the eggs are produced, and it, too, is accompanied by tubes and other structures for the reception of sperm and the conduction of the eggs and, in mammals, for the protection and nourishment of the developing embryo.

Other Functions of the Sex Glands

In birds and mammals the testes and ovaries produce not only the germ cells, but they also secrete into the blood stream certain chemicals known as *hormones* on which depend the development of many of the secondary sexual characters. After early removal of the testes in man for example, the voice remains high as in boyhood, the beard fails to grow, and many of the sexual differences are minimized or extinguished. Such castration effects are very marked in birds. If the ovary is removed from a young chicken of a breed in which male and female differ greatly in plumage, form, and color, it develops the bright plumage of the male and grows a large male-like comb. Castration of the male produces the capon in which the male comb and some other male characteristics fail to appear (Fig. 29).

Many of the marked psychological differences between the sexes are also known to depend on the presence and proper functioning of the primary sex glands. The complex sexual differences in these animals are thus members of a chain of which the first link is the testis or the ovary. The fundamental question therefore is: What is it that determines that in one individual a testis shall develop, and that in another an ovary shall appear?

The Chromosomes in the Male and Female

The clue to the first and decisive event which leads to this difference has already been mentioned. It was the discovery that the sexes in many species of animals (and perhaps in most) *differ in the kinds of chromosomes* which make up the nuclei of their cells. Generally all of the chromosome pairs but one are identical in the two sexes, and, of course, this must be so, because both male and female exhibit all of the hereditary characters typical of their species and variety, and these we now know are transmitted equally from both parents through the chromosomes.

But in man, for example, one chromosome pair is different in the male and in the female. All of the cells of the female have twenty-three pairs of chromosomes which seem to be identical with those of the male, plus a peculiar pair known as the X, or sex chromosomes. The male has twenty-three pairs plus only *one* of these X chromosomes. Its mate in the male has a different appearance and is known as the Y chromosome. Since all other pairs are alike in both sexes we may briefly describe the female as XX (two sex chromosomes) and the male as XY (one sex chromosome).* When the gametes (eggs) are formed in the female, each with one member of each pair of chromosomes, one member of the X pair passes into each egg. All eggs, therefore, have an X chromosome. In the male, however, since there is only one X, only half the sperm can receive it after the reduction division, and the other half gets its mate, the Y chromosome. Every egg, then, is the same, but the sperm are of two sorts in equal numbers. At any fertilization there is an equal chance of an egg being fertilized by an X or a Y sperm. Below are the results of these two types of union:

egg with *X*, fertilized by sperm with *X*=XX female
egg with *X*, fertilized by sperm with *Y*=XY male

When Is Sex Determined?

The sex of the child is thus determined by the kind of sperm which happens to fertilize the egg. Since the two types of sperm are produced in about equal numbers the chances are about equal that a male or female will result from any given fertilization. In the long run, the numbers of these two types of union should be about equal, and it is true that about half the children born are boys and half are girls. The numbers are generally not exactly equal, for the number of boys born slightly exceeds the number of girls—about 105 to 100 in the United States. This may be traced to some slight advantage which the Y sperm enjoys in fertilization, or to different mortality of boys and girls at some time before birth—but this is another problem. It does not alter the essential fact that the sex of the child is apparently settled at the moment of fertilization by the type of sperm which fertilizes the egg.

* See Figure 17.

Some Interesting Proofs

The study of human chromosomes under the microscope does not bear the whole brunt of the proof of this mechanism. It was, in fact, the last proof to be supplied. Earlier it had been found that a number of human traits were inherited in the peculiar criss-cross or sex-linked fashion, like white eyes in Drosophila. Color-blindness or inability to distinguish red from green is such a trait. A color-blind male transmits his defect only to his grandsons through his daughters, never to his sons, but a color-blind mother, even though her husband is of normal vision, always transmits her defect to all her sons (Fig. 31). This is precisely the mode of transmission of the X chromosome in man, and a sex-determining X chromosome bearing the genes for these traits had to be assumed to explain this type of heredity even before it was discovered under the microscope. Finally, it was known that occasionally twins are born which are almost identical. These arise from a single egg which produces two embryos. Such twins are always of the same sex, either both males or both females (Fig. 32). If sex were *not* determined at fertilization, these twins should be of opposite sex just as often as are ordinary twins which arise from two eggs.

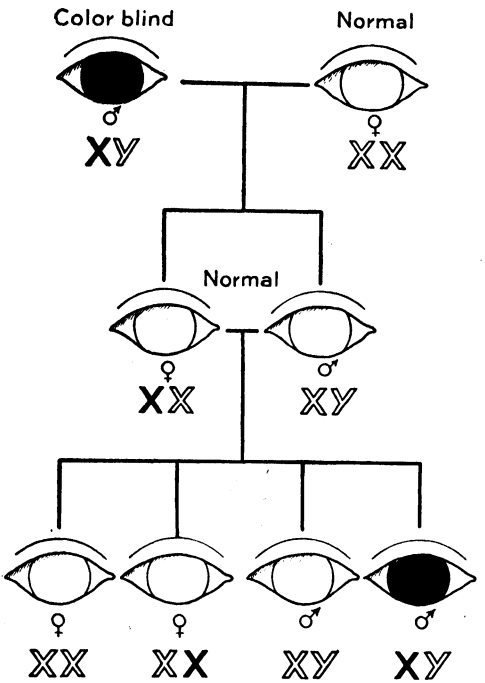


Fig. 30—THE INHERITANCE OF COLOR-BLINDNESS

A color-blind male mated with a normal female. The color-blind male transmits this defect through his daughters only and it appears only in his grandsons since their Y chromosomes contain no dominant normal gene to hide their X chromosome gene for color-blindness. The inheritance of this character discloses the distribution of the *X*, or sex, chromosome to the gametes and progeny. *X* chromosomes carrying the gene for color-blindness are shown in black

From a drawing by Mabel B. Little

Control of Sex

As soon as it was recognized that the sex of the human offspring was to be ascribed to the type of sperm which fertilized the egg, many ancient beliefs about the cause and control of sex in man withered and died. The nutrition of the mother and other conditions surrounding the embryo during growth were seen to be impotent to affect its sex, since this had already been settled at the moment of fertilization. New speculations arose to take the place of the discarded ones, for it was evident that all that was required to control sex was to control the proportions of X and Y sperm. If only Y sperm were available for fertilization, male offspring would be produced; and if the supply could somehow be limited to sperm containing the X chromosome only females would result.

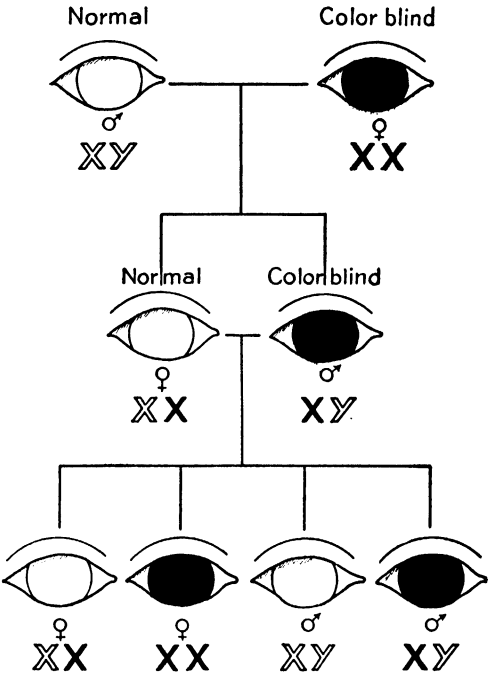


Fig. 31—THE INHERITANCE OF COLOR-BLINDNESS

A normal male mated with a color-blind female. The color-blind female transmits her defect through her sex (*X*) chromosomes to both sons and daughters. The defect appears only in the sons because the daughters receive a normal (dominant) gene in the *X* chromosome from the father, while the *Y* chromosome does not carry the normal gene

From a drawing by Mabel B. Little

This is a good possibility in theory. Actually there is as yet no way of separating these two types of sperm or of altering their proportions. The hopes of some investigators rest on the possibility that the two sorts of sperm may react differently to physical and chemical conditions within the body of the female, and that under some conditions only one sort may survive to effect fertilization. There is no good evidence as yet that this is so, nor is there truth in the claim that sex in man may be thus controlled at present, but the knowledge of the

mechanism by which sex is normally determined may lead eventually to some method for consciously influencing the proportions of the sexes at birth.

Sex Determination in Animals and Plants

This description of sex determination in man is merely illustrative of a general type which is common in the animal kingdom and in some plants. Although many insects (*e.g.*, Drosophila), some fish, and some amphibia (frogs) follow the same scheme and produce two kinds of sperm, in birds, moths, and a few fishes the situation is reversed and the sperm are all alike, but the eggs are of two types, one of which always produces females, the other always males. In some animals (*e.g.*, bees) the males develop from unfertilized eggs by true virgin birth, or *parthenogenesis,* and have only half the number of chromosomes of the females which come from fertilized eggs. In all these variants of the process, sex is the result of differences in chromosomes and thence of the genes which they carry.

A new chapter in the story of sex is being written by the

Fig. 32a—IDENTICAL TWINS

These twins were separated as babies and lived in different environments for seventeen years. Their great similarity is due to their identical heredity since both arose from a single fertilized egg. Identical twins are always of the same sex

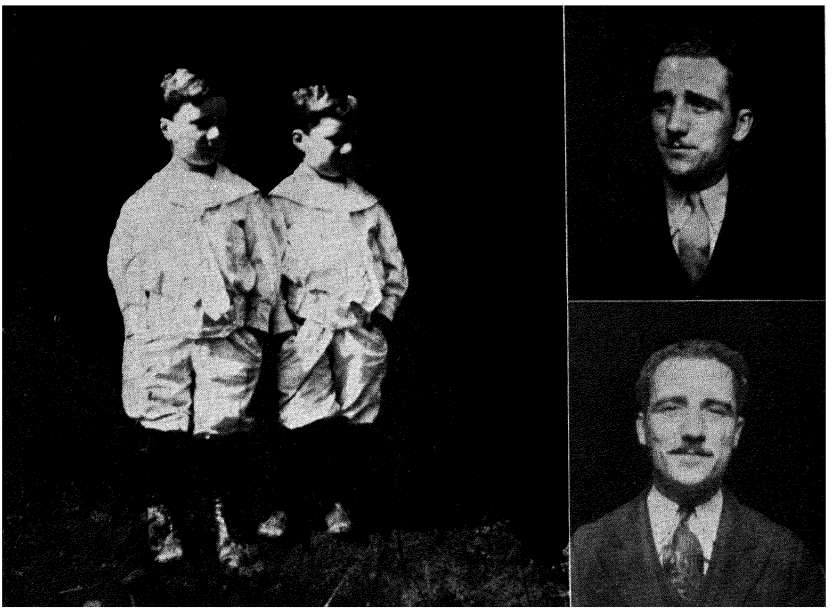


Fig. 36b—IDENTICAL TWINS
left, at age of five; *right*, at age of twenty-one

studies now going on of the way in which the original differences in chromosomes and genes are translated into the great differences which ensue in the adult animal; of how other chromosomes besides that peculiar one—the X—contribute their quota of effect in influencing development; and of how the sex glands in the higher animals, appearing first as a result of the hereditary constitution of the individual, later through the blood stream, influence the whole physical and mental nature of the organism. These new ideas will in time once more transform our outlook; but they promise to confirm rather than to alter the conviction which biologists now have, that sex, like other characteristics of the animal, is the result of the operation of an orderly mechanism, regulated by laws which are in all ways similar to those concerned with heredity.

CHAPTER VI

THE ORIGIN OF VARIATIONS

IN the first chapter of this book we set out to discover the reasons for resemblances between parent and offspring and by extension for those continuing likenesses that run so persistently through the generations of men and other forms of life. We found that the theories of genetics, resting on a wealth of facts established by experiment, require us to conceive of these general resemblances as the sum of many specific and particular ones, which are transmitted by an exact mechanism of reproduction. This mechanism operates according to orderly laws which describe the outstanding facts of heredity. These laws were discovered through the study of differences or departures from type which had arisen during the history of the races of animals and plants.

Two Vital Questions

During that excursion into the realm of genes and chromosomes two vital questions were continually presenting themselves. First, how do these variations, these hereditary differences, originate? Whence came the *first* white mouse in a race of gray ones, the *first* white-flowered pea plant, the *first* blue-eyed man, or the *first* color-blind man? Secondly, what part does the environment play in molding the characters of living things, and especially in the origination of new characters? Our discussion of heredity was all in terms of factors within the organism, but this limitation was artificial and for purposes of simplification only. It is obvious that animals and plants do not live in a vacuum, but in a variable environment on which they are dependent for their whole means of subsistence and to which they must continually adjust themselves by changing their forms and their habits. The hereditary factors constitute only half of each

reaction; they supply the internal locks in which the keys of the environment turn.

The Answers to the Questions

In inquiring what answers modern genetics can supply to these questions, many old and related puzzles must be re-examined. The perennial debate on the inheritance of acquired characters; the opposition between heredity and environment, which rests on mistaken notions both popular and scientific; the mode of origin of new species; and the mooted questions of the methods of progressive evolution, must all be considered. In the short scope of one chapter scant justice can be done; and it is to be remembered that our knowledge of these matters is far from perfect. They are only just reaching that state where we can begin to consider them on a par with other scientific questions, and extended discussions are likely to go beyond the facts.

The Problem of Environment

To many people the most obvious source of new variations has been in the changes which appear in the body in response to changes in the environment. The belief that such new or acquired variations may become hereditary has been widespread. That specific conditions of life induce specific variations no one can deny. Bad food or too little food may produce under-development and permanent stunting and other abnormalities; continued absence of a single minor constituent of the diet may result in marked disorders, *e.g.,* goitre if iodine is not present in the food, or rickets in the absence of one of the vitamines or of sufficient sunlight.

Continued physical exercise leads to greater muscular development just as continued use of the mind enlarges its capacity and abilities. Wearing clothes, living in houses and in cities, and other conditions of the domestication of the human animal, all change him in body and in mind. Most remarkable fact of all he may acquire immunity to specific disease, either through recovery from the disease itself or by inoculation with preventive sera. *Are these changes in the parent which arise in response to changes in surroundings transmitted as such to the offspring?*

There is a curious desire in many people for an affirmative answer to this question, and the frequent "proof" of such an answer has often appeared very much like a wish-fulfillment pure and simple, and this, coupled with the ambiguous form in which the question is often phrased and the difficulty of testing it experimentally, account for the contradictions and prejudices which have marked the discussion. How comforting it would be to know that our own improvement, so hardly won, could be passed on to our children—to know that we could relieve them of the labor of learning their letters by a diligent cultivation of our own minds—to know that we could benefit permanently the men and societies of the future by bringing ourselves and our surroundings nearer to perfection!

An affirmative answer would also seem to be favored by the long panorama of continuous adjustment to varying environments which constitutes the evolutionary history of man and other creatures; and at first glimpse this answer would appear to simplify and to solve the chief problem of evolution. But we must remember that we have to explain not only change but also continuity of type—the tough persistence of specific form and function by which, for example, the Negro, removed from his tropical environment into the alien north, preserves for centuries the essential features of his race. This question, like so many others, is not to be settled by appeal to general arguments, but by evidence from specific cases designed to test the questions at issue.

What Are the Facts?

It is clear that in the higher animals and plants inherited characters are those which arise from genes in the reproductive cells. To become transmitted therefore any new character must become represented in these cells. Do characteristics newly acquired by the parent so specifically affect the gametes that they continue to appear in the descendants in the absence of the conditions which first called them forth?

At the outset we must split a hair by explaining that the passage of a substance through the gametes does not always mean that it is inherited in the narrow sense of depending on a permanent gene or determiner in the chromosomes. Thus a

fatty dye injected into a hen may appear in her eggs and even in her chicks although it disappears in the next generation. Syphilis is due to a specific parasite—a minute spirochaete—and this is able to pass through the egg from an infected mother to her child. Other diseased conditions are acquired so early in development and appear so frequently in the offspring of diseased parents that they may be spoken of as "inherited" if the word is used in the loose sense of implying mere passive transmission. But this is certainly not the way we inherit the specific characters of our mind and body.

We must also lay at rest the old bogey of maternal impression in man and mammals in which the embryo develops within the body of the mother. A vast body of human myth and the lore of animal breeders insist that certain unusual characters such as birthmarks are caused by specific experiences of the mother during pregnancy. The farmer whose black cow kept in a red barn gave birth to a red calf kept this quaint superstition alive. But the fact is there is no evidence of a cause and effect relationship in any of these cases. The embryo lives within the mother almost as a parasite, into which nourishment passes from the mother's blood by seepage through a membrane. Within the mother's blood antibodies protecting the child against disease may occasionally pass into the embyro, but this is a temporary and not a permanent protection, and corresponds only to an inoculation given by the mother to the child. Except for this possibility and for food, the embyro develops according to its own hereditary constitution.

Putting these cases aside, what evidence is there of the inheritance of environmental variations? The most frequent claims have been made for inheritance of the changes wrought by use or disuse of parts, including the mind, by poisons or stimulants such as alcohol, by changes in amount and kind of food, and by mutilations. The French zoologist Lamarck, who first organized the affirmative side of this debate and after whom the belief in the inheritance of acquired characters became known as Lamarckism, brought forward arguments from his wide biological experience to show that all organisms responded directly to their environment and to new physical needs and that these responses were passed on in a cumulative way by the descendants;

that a sufficient stimulus to the development of a new part was the *need* which the animal felt, and that variations thus arising were transmitted together with those arising from use or disuse. Darwin accepted many of these ideas and incorporated them into his theory of the origin of variations.

In the latter half of the nineteenth century arose a vigorous champion of the negative view, August Weismann, who marshaled the evidence against the inheritance of any of these effects, for the first time made a strict classification of new variations of animals and plants into those which are hereditary and those which are not inherited at all, and appealed to new facts to show that for animals at least there was no mechanism by which the new bodily variations could get into the hereditary material, or as he called it, the germplasm. This isolation between the body or *soma,* whose variations are temporary and die with the body, and the *germplasm* which is perpetuated through the reproductive cells, was dramatically demonstrated by a famous experiment performed by Professor William E. Castle, of Harvard University, in 1910. With the assistance of Dr. John C. Phillips, he transplanted the ovaries of a black guinea pig into a white guinea pig whose ovaries had been removed. The white guinea pig (with "black" ovaries) was then mated to a white male. All such matings of white by white in guinea pigs produce only white offspring for white is recessive and breeds true. But this mating produced only *black* young, exactly like those produced by black guinea pigs. The "black" germplasm had been entirely unaffected by its residence in a white body.

The battle aroused by this distinction between soma and germplasm and by the negative evidence of August Weismann and others has waned somewhat of recent years, but in most respects Weismann appears to be the victor.

The Question of Mutilations

It is now clear that bodily mutilations are not inherited. First, there is the evidence that the long continued practices of many peoples, the circumcision of the Jews, the binding of the feet of Chinese women, the docking of the tails of sheep and horses, the dehorning of cattle, have had no effect whatever on

the descendants, and there are also direct experiments with animals which give a negative answer.

There is likewise no evidence that such physical differences as skeletal or muscular changes due to occupation or to athletic training, are inherited. There are some unexplained questions, as, for example, why the soles of a baby's feet are thickened even before he walks on them, but in the absence of direct evidence in favor this question may also be answered in the negative.

Inheritance of Effects of Training

With mental acquirements the case is not quite so clear, although since we must all begin our learning at about the same point from which our parents started there cannot be any considerable transmission of their acquisitions. Whether offspring from trained parents learn more quickly than those from untrained ones has been tested by experiments with mice and rats. These animals may be trained to go through a maze in search of food, or come for food at the sound of a bell. In some experiments the offspring of trained parents seem to require less training in order to learn these things than do the offspring of untrained parents. The question is not so simply settled, however, for several other experiments, more critically performed, gave negative results. This type of experiment is full of pitfalls, for there are innate differences in educability to be reckoned with, differences in docility, acuteness of sense perception, and many others. At present this claim of inheritance of acquired training must be regarded as unproved.

Effects of Poisons

The same verdict holds with respect to the effects of various chemical substances such as alcohol and poisons such as lead. Many generations of many animals have been repeatedly made drunk in the attempt to discover whether alcohol gives rise to new and presumably deleterious variations in the offspring, but the evidence here is negative. Alcoholic parents may have fewer offspring, but in some cases the offspring were superior to those from non-alcoholic parents, which seemed to indicate that excessive amounts of alcohol in the system might kill off the weaker germ cells and leave only the stronger ones to beget progeny.

There is some evidence of uncertain value which shows that hereditary changes in some animals may arise as the result of introducing into the blood stream of the mother antibodies which attack specific structures of the embryo such as the eye, and that these may be permanently inherited.

Although possibilities such as that last quoted should make us chary of drawing too sweeping a negative conclusion, it is nevertheless safe to say that in no case has adequate proof been provided for the inheritance of any of the bodily acquirements just discussed. On the other hand there is good evidence that the characters for which we can establish not only the fact but the mechanism of inheritance have arisen in other ways.

Origin of New Characters

It is quite plain now that the hereditary variations which have been studied are due to something inside the organism. Most of the characters which we have used in illustrating the mechanism of inheritance take their origin in genes which are located in the chromosomes. So far as we know there is no other general method of inheritance. By and large, then, heritable variations are due to genes. How now shall we explain the appearance of new heritable variations, and—most vital question of all—how do new genes arise?

Recombinations of Old Characters

An answer which has become more and more obvious is that many of the variations which we see for the first time in plants, animals, and men are not new at all, but are *reappearances* of old traits which have been present in the stock for generations as recessives, and only come to light when two parents, each carrying the recessive gene, are mated. The red and white calves which occasionally appear in pure bred herds of black and white Holstein-Fresian cattle, the birth of children with hereditary defects to normal parents, etc., represent such segregations of recessive traits, even though the abnormal ancestor was many generations removed. Likewise new *combinations* or *recombinations* of genes are continually occurring, as when black mice crossed to white ones produce gray offspring unlike either parent.

Hybridization or the crossing of races, species, and varieties

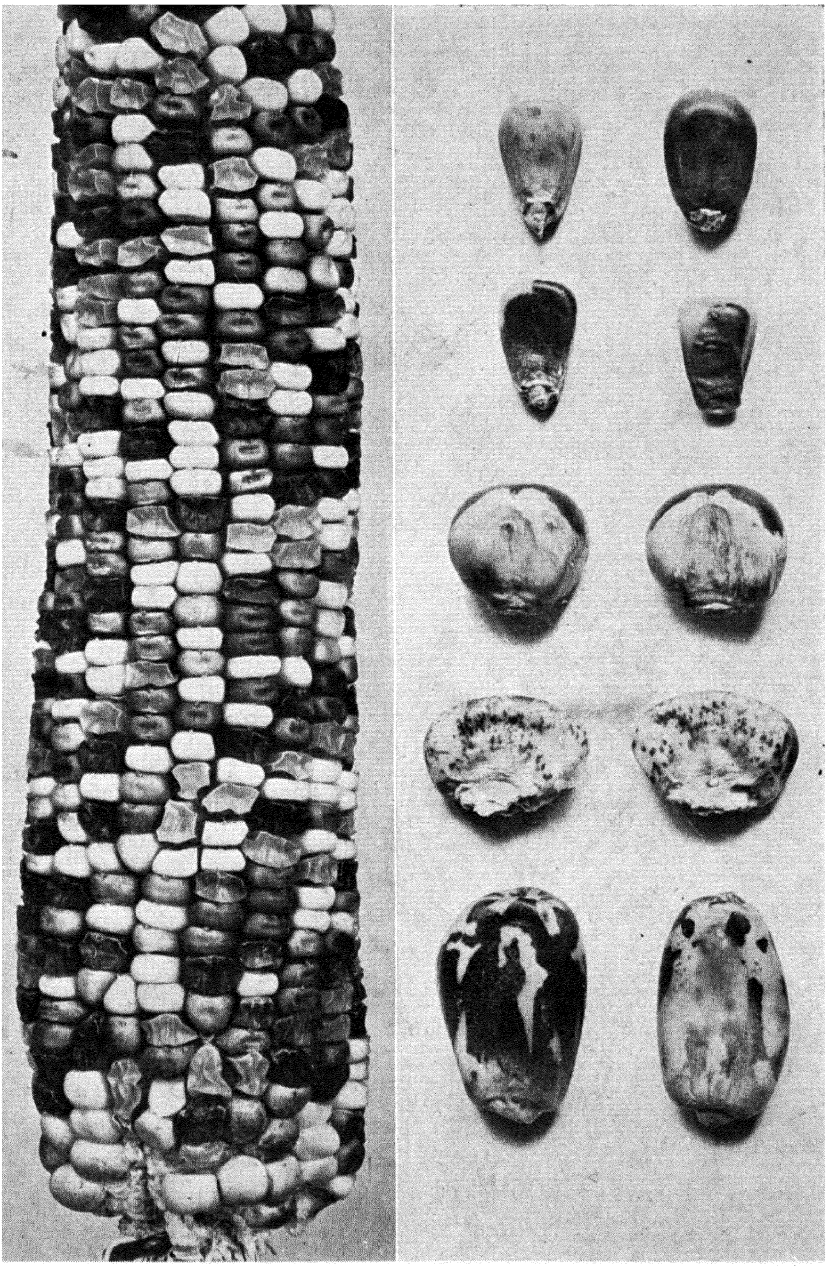


Fig. 33—VARIABILITY DUE TO RECOMBINATION

Left, Common seed variations in maize; *right,* variation in color, pattern, form, and size of corn kernels

is a potent source of such new combinations, and it is a fact familiar to farmers that the offspring of hybrids or mongrels are distressingly variable (Fig. 33). With increasing ease of travel and constant migration of races the human population is gradually becoming more mixed and more variable, and where many races meet and mingle (as in Hawaii) one can find human types never before seen under the sun—the woolly hair of the Negro with the slanting eyes and folded lids of the Oriental, the blue eyes of the European, combined with the beautiful skin color and physique of the Polynesian. Thus cross-breeding maintains and even increases average variability by making new combinations possible, but it does not provide *new* or *original* variations.

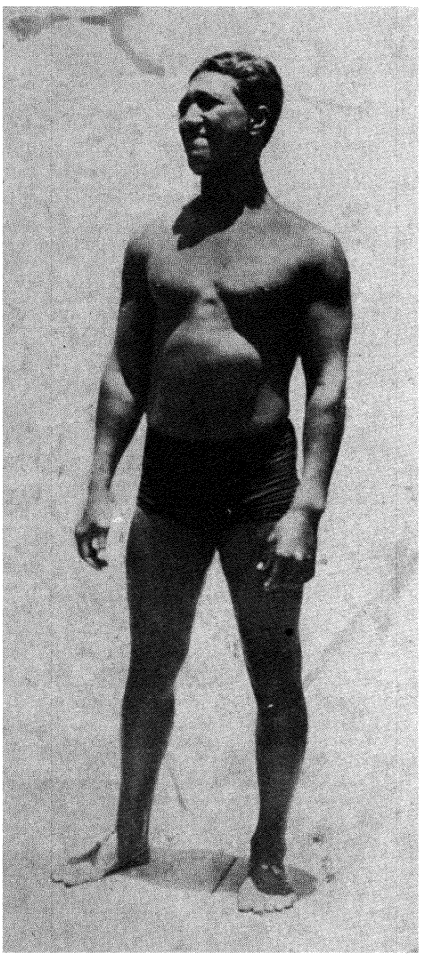


Fig. 34*a* A FULL-BLOODED HAWAIIAN
Photograph from Prof. A. M. Tozzer

The Appearance of "Sports"

By far the greatest interest and importance attaches to those sudden and hitherto unexplained changes by which a really new hereditary character suddenly appears. Naturalists and farmers are not unacquainted with such cases which they have usually called sports or freaks.

One famous case occurred in Massachusetts in 1791 when a lamb with short bent legs was born in a flock of normal sheep (Fig. 35). No other sheep like this had been known; it was startlingly new, and it transmitted its peculiarity by inheritance

so truly that a whole breed of short-legged sheep—the Ancon breed—was established from the descendants of the original sport. At one time these were popular in New England, because they could not jump the low stone walls of the pastures. The short-legged trait was apparently inherited as a recessive. Many other similar instances are known in both animals and plants. Darwin recognized such sudden changes as a possible source of the new variations, from which nature chose the most successful to survive, although he thought that such changes, by their sudden and radical departure from the type, would often unbalance the harmonious adjustment of the parts of their possessor and might be more likely to handicap than to improve his chances in the struggle for life.

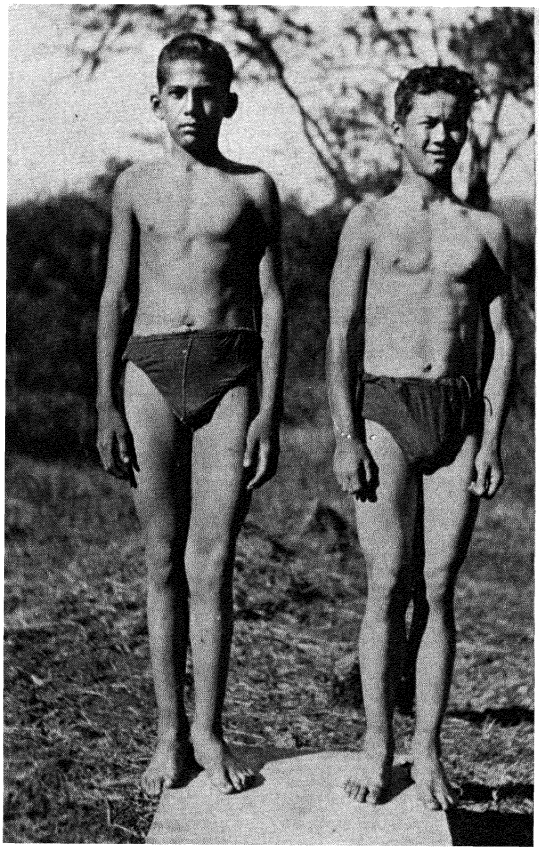


Fig. 34b—NEW RACIAL TYPES BY RECOMBINATION

Three races—Hawaiian, Chinese, and Irish—mingle in the boy at the right; the boy at the left is the son of a German father and an Hawaiian mother.

Photograph from Prof. A. M. Tozzer

MUTATIONS

Then came Hugo de Vries, the great Dutch biologist, who not only rediscovered the laws of Mendel but also introduced into biology new ideas concerning the origin of variations. De Vries was impressed by several facts about the variations found

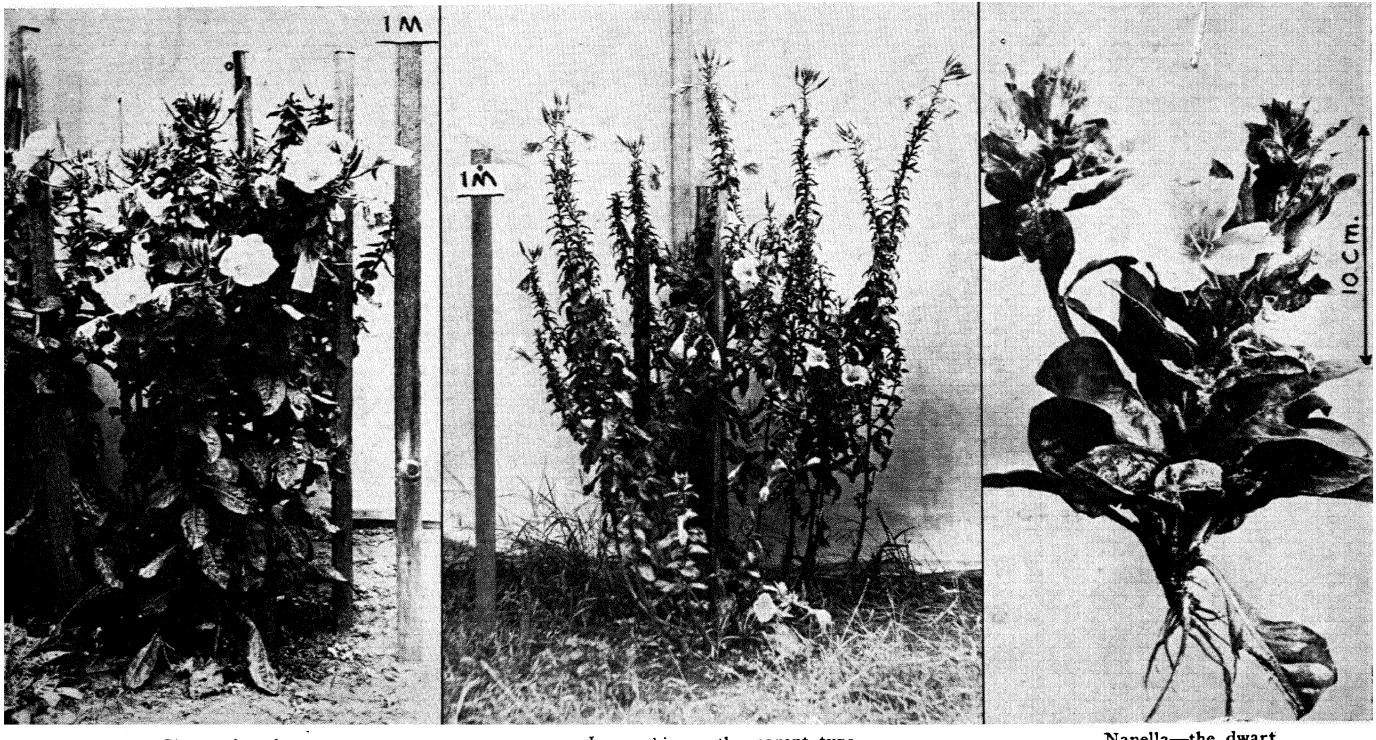
Courtesy of Storrs Agricultural Experiment Station

Fig. 35—A NEW INHERITED VARIATION WHICH AROSE BY MUTATION

An Ancon short-legged sheep on the left and a normal sister on the right. The original Ancon variation appears to have died out completely toward the end of the last century. But about 1925 another short-legged sheep was discovered on a farm in Norway, representing apparently a new Ancon mutation which had appeared over one hundred years after the first. The flock in which this occurred was purchased and brought to the United States by the Connecticut (Storrs) Agricultural Experiment Station, and from it a new Ancon variety is being established.

in nature, and especially those which appeared in the evening primrose of which he bred large numbers under close observation. New heritable variations in pure races were in the first place quite rare; and each one seemed to arise by one discontinuous jump from the parent type, which led De Vries to call them *mutations*. These new types bred true from their first appearance, usually represented rather a considerable change from the parent type, and were quite independent of environmental changes. From the evening primrose in De Vries' garden arose giant and dwarf plants, some with smooth leaves, some with red veins, and others with other striking differences. To such sudden changes—mutations—De Vries ascribed chief importance in explaining the appearance of new variations in nature and the origin of new species. They seemed to him to be sudden changes in the hereditary material itself, and as he could not discover what brought about these sudden upheavals within the organism, he declared them to be spontaneous.

It now appears that such sudden changes within the heredi-



Gigas—the giant

Lamarckiana—the parent type

Nanella—the dwarf

Fig. 36—A FAMOUS PLANT, THE EVENING PRIMROSE (*OENOTHERA LAMARCKIANA*) AND TWO OF THE NEW TYPES (MUTANTS) TO WHICH IT GAVE RISE

It was chiefly upon evidence from this plant that DeVries founded his theory of evolution by discontinuous variation (mutation)

From photographs of plants grown and studied by Dr. Bradley M. Davis

tary machinery are the chief sources of new variations. To say that they arise spontaneously is merely to admit that we do not yet know what causes them, although, as we shall see, our ignorance on this matter is not quite so dense as it was a few years ago. Mutations have now been observed and studied in many species of animals and plants. They are found to consist of several kinds of changes in the chromosomes, but most frequently the new mutation is found to be a sudden change in a single point on a chromosome, as though some tiny bit of living stuff had undergone some sudden rearrangement of its parts. This event announces the birth of a new gene.

The Results of Laboratory Observation

The origin of several hundred new genes has been recorded in the vinegar fly Drosophila which has given rise, under close observation in the laboratory, to a great variety of new variations, most of them inherited as single gene differences in orthodox Mendelian fashion. New varieties have appeared with white eyes and eyes of many different colors, with half eyes, or no eyes at all; with bent, shortened, blistered, and otherwise abnormal wings, or with no wings at all; with changes in body colors and in the most diverse and minute aspects of the animal. Similar changes have been observed in other animals and plants bred in closely controlled pedigreed cultures, but not in such quantities as in Drosophila because these changes are rare and it is not possible, under the rigid conditions necessary, to observe several million individuals in very many kinds of animals or plants.

The Frequency of New Genes

In general, the origin of new genes by mutation has been found to occur with measurable, although low, frequency. The occurrence of a few hundred mutations in thirty odd million individuals does not indicate a very high percentage of new genes. Gene mutations, we learn also, are not to be defined by the size of the change they produce in the body. They may be barely perceptible as in some of the minute changes in one or a few of the hairs of Drosophila which nevertheless Mendelize perfectly. Finally, they seem to occur quite at random, and there is neither

rhyme nor reason to the changes for which they are responsible—head, limbs, wings, brain, instinct, longevity—any of these may suddenly be drastically modified by a new change. The process seems to be as casual as a stroke of lightning. Nor is it particularly comforting to know that few of the new genes which have arisen by mutation, in Drosophila or in other species, represent much of an improvement over their parents. Most of them are distinctly deleterious and are actually lethal, killing the individuals which get two of the new genes just as the pure yellow mouse is killed before birth. This is a casual, wasteful method of nature, by which there appear hundreds of new variations which die to one which may represent some slight improvement.

What Happens when a New Gene Arises?

Just what is it that happens when a new gene arises? Many anxious biologists would like to know the answer, for this would lead directly to some of the deepest secrets of life. Since genes seem to be parts of the chromosomes it would seem that some bit of the chromosome, perhaps a molecule, is suddenly changed into something slightly different. We know the white-eyed fly arose suddenly from the red and behaves in inheritance as though it contained a gene for white at a point on the sex chromosome which the geneticist defines as 1.5 units from the upper end. When this point was "normal" as in the wild fly, the fly had red eyes. Suddenly a change took place, and at some cell division one of the daughter chromosomes had a gene for white at this point. This changed chromosome passed into a sperm or egg cell and thence into a new individual. When this new fly was mated with a relative which had also received the changed chromosome, two white genes came together and the first white-eyed fly appeared. This has probably occurred countless times in nature. There are, therefore, some reasonable ideas as to *where* the changes take place—but still we ask, what causes them?

Artificial or Induced Mutations

There have been many attempts to make mutations occur artificially, but it was not until living things were subjected under

very special conditions to that most artificial stimulus, the energy from X-rays and radium, that any positive results were obtained. Now by bombarding either the reproductive cells or the whole animal or plant with the barrage of electrons generated from these potent sources of energy it is possible artificially to induce new mutations in their descendants (not in themselves).

As Professor Herman J. Muller, of the University of Texas, the first geneticist to employ this method successfully, has said, it is now possible to transmute the gene. When, for example, vinegar flies are exposed to rather stiff doses of X-rays (stronger than those used in X-ray photography or in ordinary medical or dental practice) the offspring of the treated flies, and especially the grandchildren, exhibit many new heritable characteristics. Most of these are due to new genes producing characters like those which had appeared spontaneously; many of them are also lethal.

The striking fact is that the treatment increases the frequency of new mutations many hundreds of times. By means of X-rays more new mutations have been produced in Drosophila since 1927 than had occurred naturally in the twenty years before, and a similar statement may be made for barley, in which Professor L. J. Stadler, of the University of Missouri, has produced new variations actually in wholesale fashion. The number of changes seems to depend on the strength of the rays, the greater the dosage the more mutations are obtained. Muller has hazarded a guess that the effects are chiefly due to chance hits on the chromosomes by the wild and erratic electrons which are sent racing through the living cells of the treated animals. A bit of the chromosome—a gene—is hit by an electron and knocked into something different. An old gene by this change becomes a new one and leads to a new character in the organism.

Practical Use of X-ray Mutations

This discovery is as yet too new to have had all its possibilities explored. There is the question, for example, whether there are sufficient radiations in nature to cause the natural or spontaneous mutations in animals, plants, and men. Can the new methods be made to yield new and improved types of valuable

animals and plants? So far its results have been to produce in abundance just those kinds of variations which had appeared with rarity before. The appearance of a new mutation seems still to be a wholly random process. When an electron is turned loose in a germ cell no man can say what will come out of it, and as yet there is no control over the kind of character that will be produced. We may be sure, however, that the ability to produce more variations at will is to be a valuable weapon in man's advancing conquest of nature, for he will be able to multiply the numbers of different characters in his domesticated animals and plants, and he should be able to pick and choose from among these in molding his creatures more nearly to his heart's (or purse's) desire.

Conclusion

Thus we come to the conclusion that the changed course of inheritance, the new variations, *arise by internal rearrangements in the hereditary materials,* and that these may be affected by certain influences from the external world. This, it must be emphasized, is quite different from the view that the environment changes first the body and then the reproductive cells, for the bodily characters of the animals or plants which are exposed to the changed condition (*e.g.,* X-rays) may be themselves unchanged, and there seems to be no direct relationship between the external stimulus and the type of mutation produced.

CHAPTER VII

THE APPLICATION OF THE NEW IDEAS

We come now to the applications of the new ideas of heredity and of variation to the problems of how living things have become so various, how species have become different; to the more immediate and practical questions of what these facts and theories mean for the improvement of the animals and plants upon which eventually we all depend for our means of subsistence; and to the prospects of the improvement of our own human kind.

Applications to Evolution

The outstanding fact in the history of life on the earth is the gradual change which has taken place in its outward forms. More complex animals and plants succeed in time those which are simpler and more primitive. The facts of this gradual development are plain and can be verified by anyone. The explanation of them is a different matter. Darwin's explanation was that all forms of life tend to multiply more rapidly than their means of subsistence; because of variation not all of these too numerous progeny are alike; some are better fitted to cope with their environment and get a livelihood; these, the better adapted, survive to reproduce and hand on their better traits by inheritance; the others have fewer descendants and eventually die out. The course of development is determined by the successful variants from type. This in a nutshell is the theory of Natural Selection.

The Meaning of Natural Selection

In the form given to it by the newer knowledge of genetics, this theory visualizes the environment as a sieve, straining out the possessors of bad or mediocre traits, and letting pass through

those which have qualities fitting them to the particular conditions which they encounter. The conditions of life seem not to create new forms; all that selection can do, either as practised by man or by the ruthless hand of nature, is to sift out the new types which arise through random changes in the hereditary material.

Species of animals and of plants and different races of men seem to differ by many genes, each with small effects, as though many new and small hereditary changes had been accumulated in the course of their long history. When crosses are made between members of distinct species of animals or plants, the most common result is complete sterility, indicating that they have become so different that the eggs of one sort cannot unite with the sperm of another. When such crosses do (rarely) produce offspring, the progeny are frequently sterile and there is evidence in some cases that the chromosomes of the two species do not pair properly in the hybrid when the germ cells are formed, probably because so many genes have become different that the chromosomes of one species no longer attract their mates from the other species. This seems to be the case in the cross of the horse and the ass which produces a sterile hybrid, the mule, which is unable, except very rarely, to form normal germ cells. Occasionally, however, successful and fertile crosses between species, varieties, or races, are obtained, and in the second generation of such crosses a complex segregation is apparent, involving differences in shape, size, skin color, etc., as though many genes, each with a small effect, were segregating at once. Although the differences between varieties and species are thus inherited in the same fundamental way as the differences between individuals, they seldom or never consist in single gene differences.

One essential factor in making possible the accumulation of different genes and the consequent differentiation of species is that of *isolation*. When two groups of related animals are separated for a time by some geographical barrier, or are prevented by other circumstances from crossing, they tend to become different chiefly because the mutations which occur are likely to be different in the separated groups. Mutations which give rise to new genes are random events, and ordinarily so rare

that the same one is unlikely to occur twice. Separated groups, therefore, accumulate different genes and become increasingly different with time.

Each species seems to be delicately adapted and adjusted to some special environment. This need for exact adjustment keeps them fairly stable, since once adjusted, any kind of a change, and especially a major one, is likely to upset this relationship to their surroundings. Perhaps this is one way to understand why most new changes—mutations—unfit their possessors for successful life and thus behave as lethals; why successful changes are so small in effect and so rare; and why the changefulness of living things in time is so dwarfed by comparison with their remarkable continuity and stability. These ideas make it a little easier to imagine how the gradual development of species may have occurred, although many of the important details of the process are still to be discovered.

Knowledge of Heredity

It is reasonable to ask: What practical benefit are we to reap from the labor, the time, and the cost expended on the experimental study of heredity? Many sciences with practical implications can plead, like many industries, that they support themselves by their by-products. The chief product of science is *ideas,* ideas which lead to understanding, familiarity with the world about us, and confidence in its dependability and order. This is a commodity with an uncertain and difficult market and one in which sales resistance is high, and most people want the more solid and consumable product, even if it is a by-product.

We need choose only a few such products from the outcome of research in genetics. They consist of new facts about the inheritance of specific defects and excellencies in useful animals and plants and of a more specific knowledge about the inheritance of human traits, of their bearing on programs of social improvement, and of the specific results to be expected from various systems of breeding in plants, animals, and men.

Application to Animals and Plants

The discovery of Mendel's laws and of the mechanism of heredity was widely heralded as presaging a millennium in agri-

culture by revolutionizing the breeding of animals and crop plants. It is plain this has not yet occurred and the application of the new methods will require a long time. Yet here and there bright spots have appeared. The varieties of the wheat plant, chief dependence of so large a proportion of the world's population, have been greatly improved in yield and quality by the careful use of the new methods. Wheat, like many other crop plants is continually threatened by diseases due to fungus parasites which greatly reduce the yield. In the United States in 1916 over 200,000,000 bushels of wheat were lost through the inroads of one variety of parasite. It has been found that resistance to infection by this parasite is inherited in ordinary Mendelian fashion, and these genes for disease resistance are now being combined with others which make for the valuable qualities desired by bakers and housewives.

Occasionally the genes influencing plant characters may be so juggled about by those who know the rules of the game that

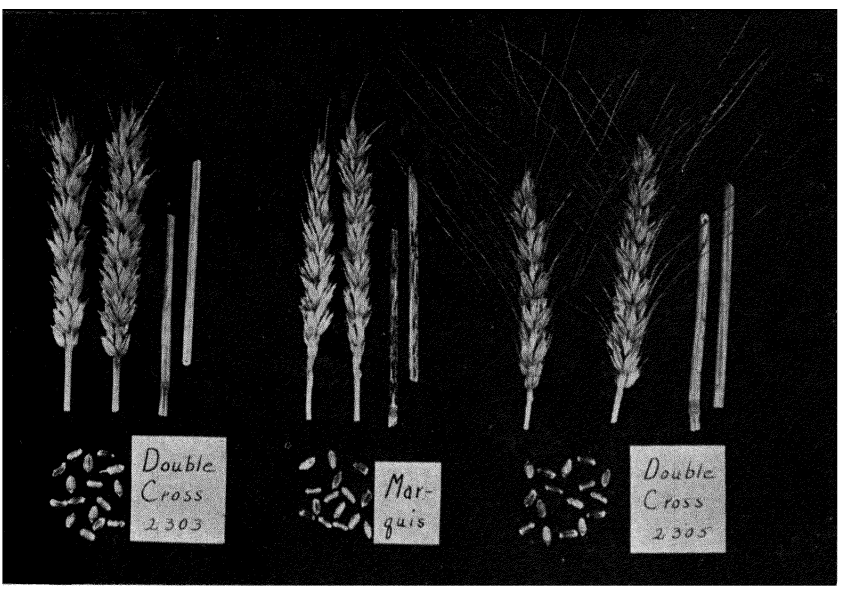


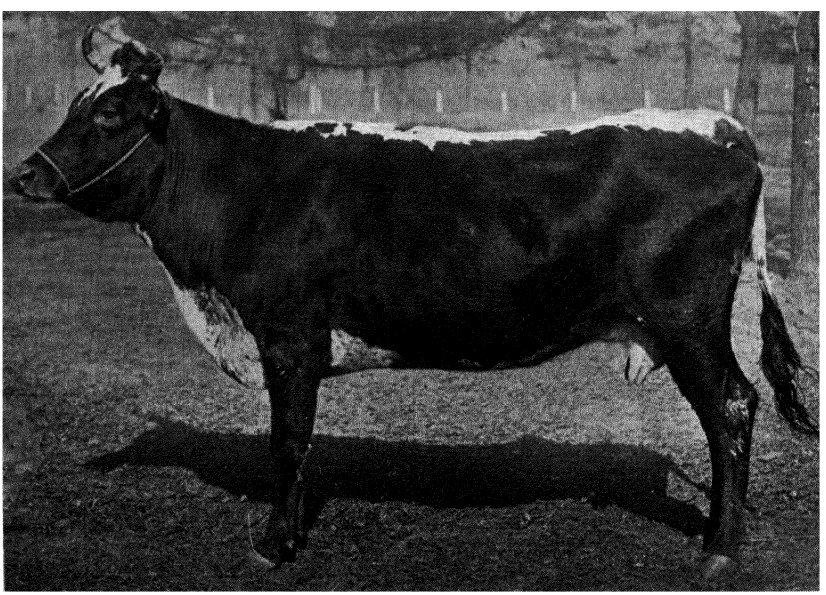
Fig. 37—EARS, STEMS, AND SEEDS OF WHEAT

Showing utilization of hereditary disease resistance in improving varieties. Marquis is a high yielding, standard variety, but is susceptible to stem rust. At right and left are samples of new varieties in which the rust resistance of another wheat species (Durum) has been combined with the other valuable qualities of Marquis

From the Department of Plant Genetics, University of Minnesota, courtesy of Prof. H. K. Hayes

new varieties may be made to order, as happened when cigar manufacturers ordered a tobacco leaf to use as wrapper which should have a special shape, size, color, texture, and flavor, and after a few years the order was filled by the delivery of a true breeding variety filling the specifications of manufacturer, grower, and smoker.

In both animal and plant breeding, the new understanding of the rôle of heredity has made the use of pedigree methods quite indispensable to improvement, and aside from the greater deliberation and care introduced into agricultural practice by this method, specific advances in yield and value of products have resulted. The leading champions in the breeds of live-stock, the best beef cattle, the cows which yield the most milk, the hens which lay the most eggs are coming increasingly from the deliberate pedigree breeders. The inheritance of so valuable a trait as egg production in fowls is understood sufficiently to allow strains to be produced which lay on an average 250 eggs a year instead of the 70 or 80 of a generation or so ago.

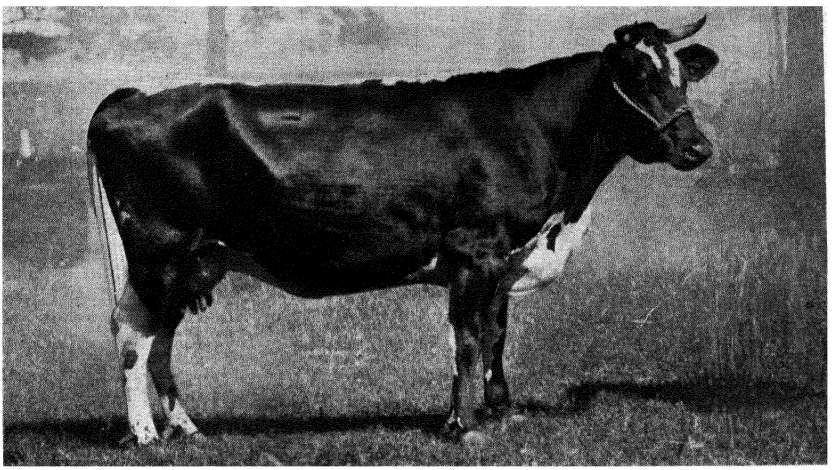


A, a scrub cow of unknown ancestry; average production, 3874 pounds of milk and 192 pounds of butter fat

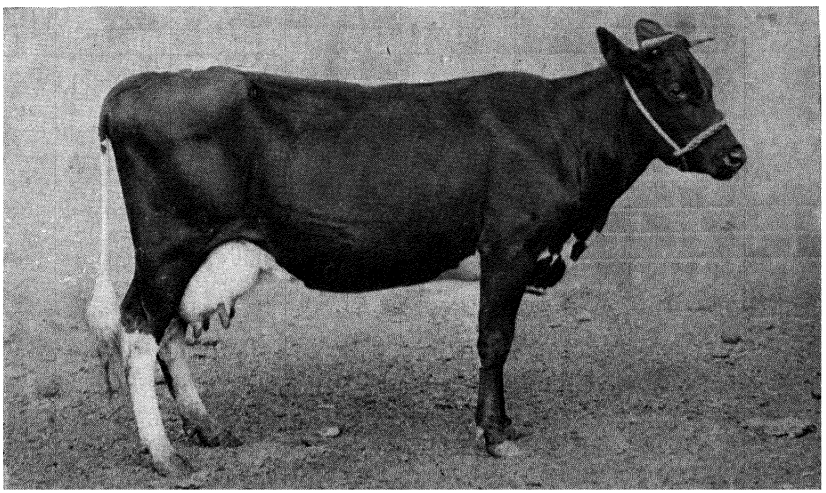
Fig. 38—IMPROVEMENT OF DAIRY

Courtesy of Dr. Andrew C. McCandlish

In animal as in plant breeding the elimination of defects and disease assumes a place of paramount importance. That resistance to specific diseases rests on the possession of specific genes has been shown in the case of that great scourge—cancer



B, daughter of *A*, after the latter had been bred to a pedigreed and selected Holstein bull; average production, 6955 pounds of milk and 266 pounds of butter fat



C, daughter of *B*, and of a purebred Holstein bull from high milk-yielding ancestry; this cow, *C*, was three-quarters purebred Holstein and gave an average of 13,366 pounds of milk and 497 pounds of butter fat

—by long experimentation with rats and mice. Some strains of cattle are wholly resistant to certain destructive parasites and this resistance may be introduced into other strains by crossing.

Inbreeding and Its Results

One of the most valuable results of the unraveling of the riddle of heredity has been in finally making clear what effect relationship between the parents has upon the descendants. That

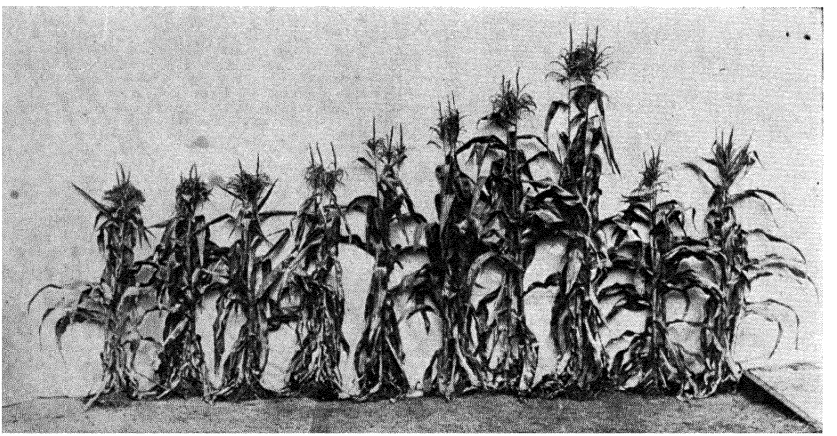


Fig. 39—THE EFFECT OF INBREEDING ON THE MAIZE PLANT

The two small inbred plants at right were crossed and the large hybrid (third from right) produced. The descendants of the first seven generations of inbreeding (right to left) show the decrease in size due to inbreeding. Reproduced from *Genetics in Plant and Animal Improvement* by permission of the author, D. F. Jones, and of the publishers, John Wiley & Sons

violent opinions have been held about inbreeding, or the mating of close relatives, is shown by the laws and customs forbidding the practice in civilized societies, and by the continual disagreement on this question among animal breeders. On the one hand, inbreeding was said to lead to degeneration of the stock and the production of monstrosities and defects; on the other, it has been frequently employed without disastrous effects in building up pure breeds. It even served as the method by which the royal family of ancient Egypt was maintained for many generations. Many plants, such as peas and beans, actually fertilize themselves, both male and female cells coming from the same flower, and these have maintained themselves without degeneration for many years. Inbreeding here seemed to be without harmful effect.

Careful breeding experiments made since 1910 have demonstrated that both contentions were correct. The continued mating of brothers and sisters for a number of generations in fowls, pigs, and guinea pigs, and the self-fertilization of the usually cross-fertilized corn plant resulted in immediate and unmistakable decline in vigor, size, and fertility, in the appearance of defective progeny, and in increased uniformity of type. In other animals, for example rats, the results were sometimes bad, sometimes good. In corn, fertilizing the silks with pollen from its own tassels and continuing this for a dozen generations resulted in a rapid decline for some seven generations, after which the strain reached a poor but constant state of growth and yield. But when two of these stunted inbred strains are crossed a spectacular recovery occurs (Fig. 39).

Hybrid Vigor

The progeny of such crosses are not only bigger and better than their parents; they may even be better than the parent strains were before inbreeding began. This great vigor is a frequent result of crossing pure types; witness the sturdy mule which is superior in many ways to its parents, the horse and the ass. The mule is sterile and this is fortunate, for the vigor of hybrids is dissipated when they are inbred. The offspring of human racial crosses often show these same excellencies. The children of Chinese fathers and Hawaiian mothers, for example, constitute one of the best types physically and mentally in Hawaii (Fig. 40). The decreased vigor and increased uniformity of many kinds of animals and plants suddenly subjected to continued inbreeding, and the unusual vigor of the direct offspring from crosses are well established facts. In order to utilize these facts and to put them to work in agriculture and human society we must know what brings them about.

The Effect of Blood Relationship

The first step in understanding them is to throw overboard the old notion that blood relationship—by itself—exercises some mysterious and baleful effect on the descendants, and to cling fast to what we really know about inheritance, *i.e.*, that there is an orderly mechanism in reproduction by which the genes are

passed on to the progeny. Relatives, it is obvious, are likely to have the same genes, received from common ancestors. In matings of relatives, like genes will more frequently come together.

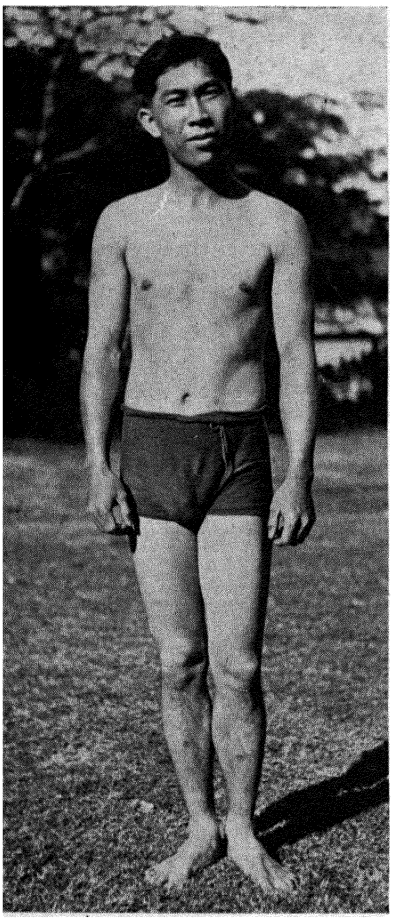


Fig. 40—CHINESE-HAWAIIAN HYBRID

Mother, Hawaiian; Father, southern Chinese

Photograph from Prof. A. M. Tozzer

Now the coming together of like genes into the same individual is the condition under which recessive genes come to expression. A recessive gene such as that for blue eyes in man may, as we have seen, be carried through many generations, masked or hidden by its dominant mate, the gene for brown eyes. But when two brown-eyed individuals mate, each of which carries a recessive gene for blue, then the hidden gene may become pure and be brought to light in some of the children. The nearer the relationship of the parents the greater are the chances that this will happen. Thus inbreeding automatically brings to light hidden recessive genes which are present in the stock.

Any long-continued system of inbreeding in this way automatically purifies the stock; it increases the proportion of pure types and decreases the proportion of hybrid types. This is the Mendelian explanation of the uniformity of inbred stocks. It explains also the frequent appearance of defects in the progeny of matings between close relatives. These are recessives which appear as the result of segregation, just as the recessive white mouse appears when two hybrid gray mice are bred together.

One further assumption is necessary to explain the general decrease in vigor which follows matings of close relatives in forms in which this is not the normal method of mating—as in man, or in fowls, or in the corn plants which usually mate with more distant relatives (outbreeding). This is, that recessive genes are more frequently harmful than beneficial and that most stock of outbred animals and plants are hybrid in many such genes which arise by mutation and are kept hidden by their dominant mates. Both of these assumptions accord with facts which we have already emphasized.

Inbreeding now appears in a different light. It simply provides the maximum opportunity for the appearance of recessive defects. If the individuals mated have few or none of these genes no bad results follow, no matter how close the relationship. Apparently the Pharaohs of Egypt, by some fortunate chance, were in this category and thus escaped the usual results, but our present laws and customs indicate that most societies were not so lucky and perhaps from bitter experience decided to prevent the mating of close relatives altogether. Inbreeding is a trial by fire which only the best stocks can survive. But once a stock has passed through this process of purification, although its excellence may be reduced, it can sustain only the damage which new mutations can do and these mutations are not very frequent. Self-fertilized plants are thus automatically pure; all recessives are immediately brought to light, and if bad, are eliminated by natural selection.

Obtaining Vigorous Hybrids

Crossing of unrelated individuals, however, brings together unlike genes. The good dominants mask or prevent the expression of the bad recessives and maximum excellence is obtained. This is temporary because when the hybrids are mated, the recessives appear and the downhill course begins.

This has important practical bearings. Hybrid vigor is now widely utilized in both animal and plant breeding. Different varieties of corn, for example, are artificially self-fertilized for several generations until they are uniform and have lost some of their bad recessive genes. Then race A is crossed with race B, producing a vigorous high-yielding hybrid. This may be

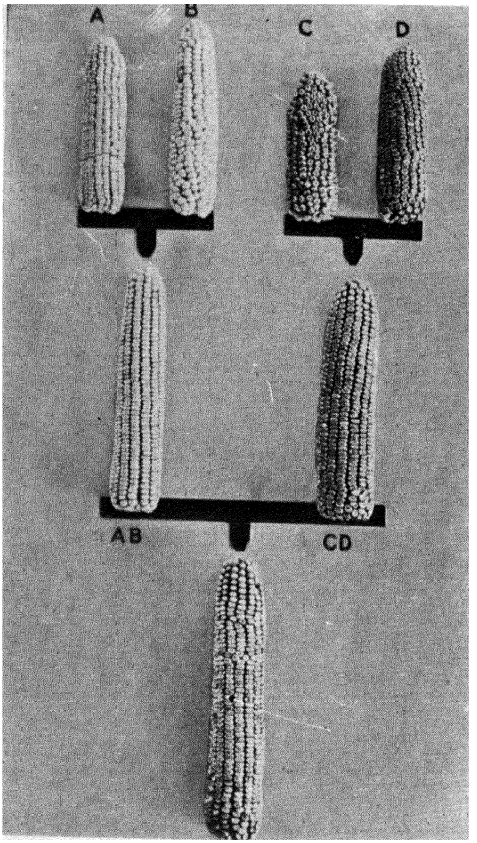


Fig. 41—THE UTILIZATION OF HYBRID VIGOR IN CORN BREEDING

Inbred strains A and B are crossed, as are also C and D, producing much greater yields of corn in the crossbred offspring. The two vigorous strains AB and CD are crossed to produce a still further increase in yield. Reproduced from *Genetics in Plant and Animal Improvement* by permission of the author, D. F. Jones, and of the publishers, John Wiley & Sons

carried further and inbred race C may be crossed with race D, and then CD may be crossed with AB and a quadruple hybrid obtained with still greater vigor. Yields have been known to be increased by nearly 200 percent over the parental averages in this way (Fig. 41). A similar system is also now beginning to be employed with excellent results, with other agricultural animals and plants, and from this unexpected application of Mendelian principles agriculture is reaping the greatest benefits in new methods of breeding.

Marriage Between Cousins

The question often arises should marriages between cousins be advised or permitted in the human family. Relationship by itself is apparently not a factor in the result. Everything depends on the particular heredity involved. In families in which defects have appeared, such as idiocy or feeble-mindedness, cousin marriages are likely to increase the number of defectives. In stocks of sound heredity, a marriage between cousins introduces no greater risk than that involved in a marriage between members of unrelated families.

Applications to Human Society

The experience of animal and plant breeders in improving the breeds of livestock and of cultivated plants by selective breeding have long offered an object lesson to those interested in the improvement of the human species itself. Plato long ago

Courtesy of The Journal of Heredity

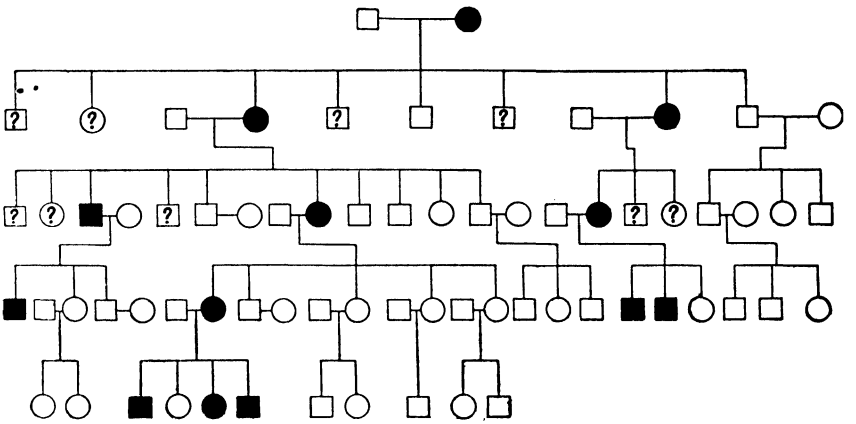


Fig. 42—INHERITANCE OF SHORT THUMBS

This pedigree chart shows the inheritance of short thumbs through five generations of one family. Squares indicate males, circles females; solid black indicates a short-thumbed person; a question mark shows an individual who died in infancy and about whose thumbs nothing is known. Connecting lines indicate marriages and children. Short-thumbed persons married normal individuals and at least one child from each of such matings had short thumbs, whereas matings between normals produced only normal children, showing that the short-thumbed condition is dominant. Matings of short-thumbed (heterozygous) persons with normals produced 12 short-thumbed and 15 normal children, a result which is very close to the 1:1 ratio expected

From a study by Dr. J. K. Breitenbecher

suggested that these same methods should be applied to the conscious production of the superior individuals who were to govern his "Republic." After Darwin had shown that evolutionary progress in all living things seems to be a result of "the natural selection" of favorable inherited traits, another English scientist, Francis Galton, brought forward a scheme for applying the same evolutionary principle to human society. Galton proposed to investigate the rôle which heredity plays in shaping human physique and intelligence and to determine what steps ought be taken by a society which recognized such facts and acted rationally in the interests of its own continued progress. The knowledge arising out of such a study he called *Eugenics,* representing a fusion of biological and sociological principles having

to do with improving the hereditary qualities of the human race.

The biological basis of Eugenics is the fact, which seems now to be sufficiently demonstrated, that reproduction and heredity in man follow the same fundamental principles which apply to other organisms. Through the efforts of Galton and of his successors, the inheritance has been traced of many human traits —physical and mental. The methods of studying heredity in man necessarily differ in detail from those employed with animals

Courtesy of The Journal of Heredity

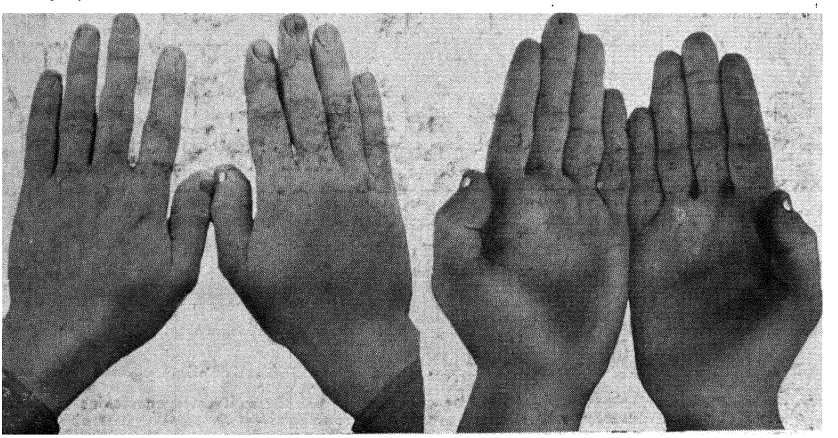


Fig. 43—SHORT THUMBS, A DOMINANT HEREDITARY CHARACTER
From a study by Dr. J. K. Breitenbecher

and plants, for controlled experiment is impossible and results must be deduced from the way in which a specific trait is distributed among the many individuals in a family tree or pedigree extending over a number of generations (Fig. 42). New principles cannot be established by such a method, but clear evidence has been obtained that human traits in general conform to the laws of segregation and independent assortment.

The nature of the traits affected is of especial importance, for social development and change are influenced largely by the intellectual and emotional natures of men. Galton's study of the heredity of mental ability, confirmed by many later investigators, showed that intellectual achievement depends on a combination of factors some of which are certainly inherited, even though in a complex way. The evidence in respect to specific mental disabilities is especially clear. Certain forms of

epilepsy, feeble-mindedness, and insanity, have been shown to rest on a relatively simple hereditary basis. Feeble-mindedness, for example, seems to segregate as a recessive character.

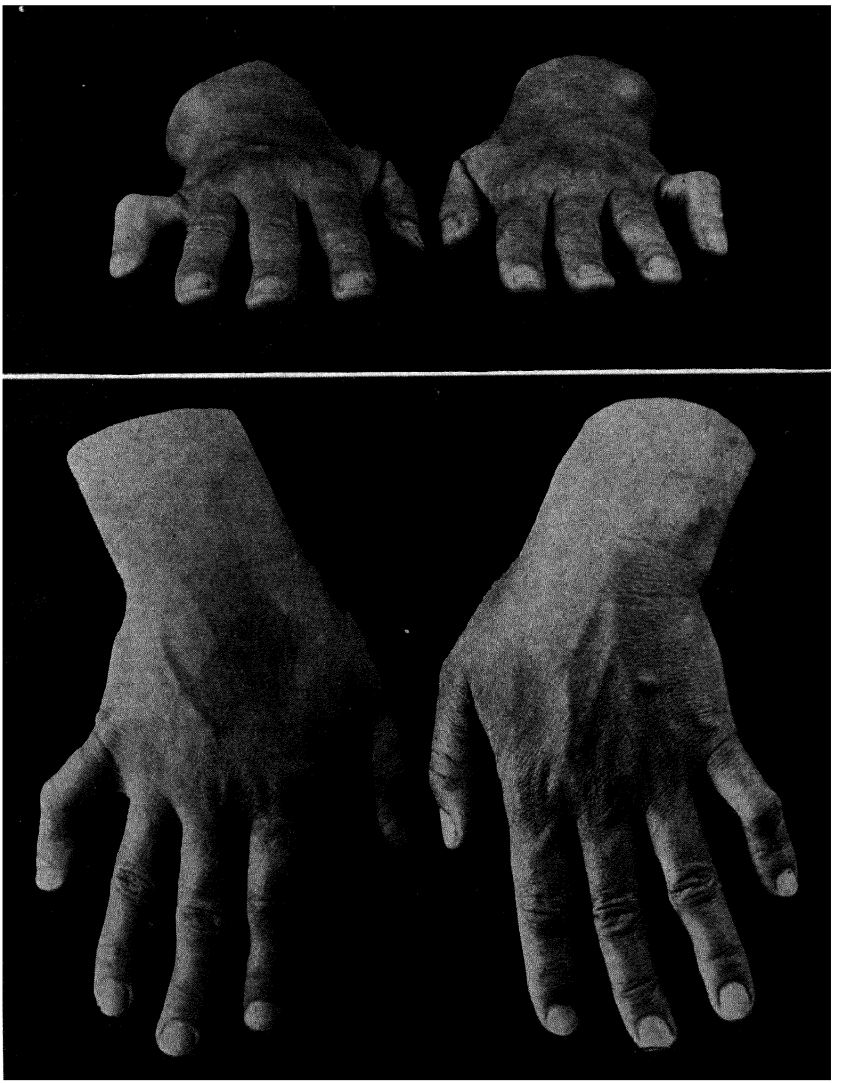


Fig. 44—CROOKED LITTLE FINGERS—A DOMINANT HEREDITARY TRAIT IN MAN

One of the tendons in each of the little fingers is probably too short to allow full extension of the finger; this peculiarity has appeared in each generation of several family histories

From Hefner in The Journal of Heredity

Normal parents, each of which carry a gene for feeble-mindedness, produce some typical feeble-minded children. Marriages between feeble-minded persons produce, with a few doubtful exceptions, only feeble-minded children.

Many physical traits—eye color, hair color, hair form, length of fingers, webbing of fingers, extra digits, albinism, and others—show simple segregation; others, such as stature, weight, skin color, head shape, apparently depend on a number of inde-

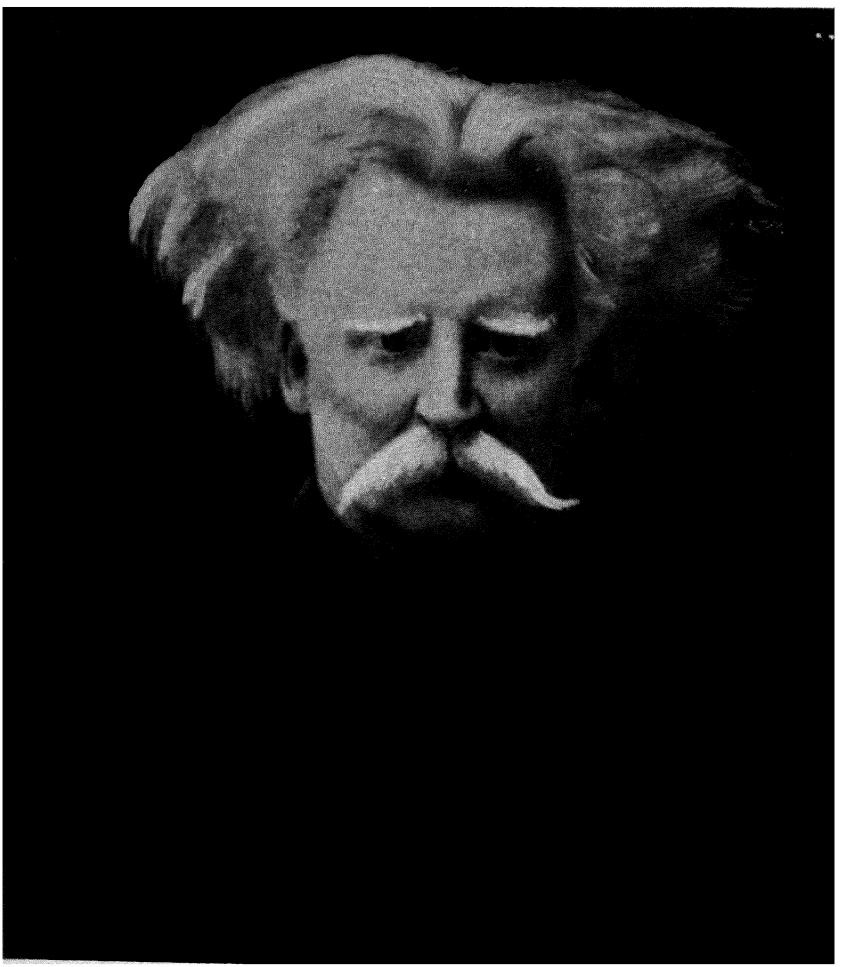


Fig. 45—THE INHERITANCE OF ALBINISM

Robert Roy was one of a fraternity of ten, all but himself pigmented—one with jet black hair. Their father had very dark brown hair and their mother sandy hair.

Photograph from Dr. C. B. Davenport

pendent genes. One of the clearest and most important characters so far studied has to do with the serological constitution of the blood. When blood corpuscles from one individual are placed in the blood serum of another (as in blood transfusion) it sometimes happens that the foreign corpuscles are clumped or agglutinated. All men can now be placed in a number of distinct classes with respect to their blood character, and these classes show clear Mendelian segregation from crosses.

Many unusual abnormal or pathological conditions have likewise been studied. Certain forms of scaly skin, cataract, night blindness, color blindness, Huntington's chorea, diabetes insipidus, bone fragility, and excessive bleeding (hemophilia) segregate as though differing by one chief gene from the normal.

On the whole it may be said of men as of animals and plants that their character depends to a large extent upon the kinds of genes which they receive from their parents.

Eugenics thus rests upon the same biological basis as genetics—the demonstrated laws of heredity.

The Need for Eugenics

The sociological aspects of eugenics have no such consistent body of principles to appeal to, yet there are social facts upon which arguments for the application of social action may be based. The chief of these are: (1) The differences in the birth rates among different classes of society; (2) The existence of a large number of physically and mentally defective persons whose care is a considerable burden upon the rest of society. Assuming that differences in social value depend upon differences in hereditary endowment, the social aim of eugenics has been to increase the numbers of the more valuable and to decrease the numbers of the less valuable. Some of the steps necessary to effect such changes have already been taken by most societies in the segregation of insane, feeble-minded, epileptic, and other defectives. The supporters of eugenic reforms would have this control, already exercised in part, extended to the prevention of reproduction on the part of those defectives, either by more effective segregation, or by sterilization (the suspension by a surgical operation of the reproductive functions of the sex glands).

Since, however, most of the defectives are not bred by defectives but appear by segregation from matings of normal persons, the eugenist advises a wide dissemination of knowledge regarding those conditions known to be a result of defective inheritance, and a more or less deliberate appraisal of the family histories of persons intending to marry and to have children, so that they may act with full knowledge of possible consequences.

Fig. 46—THE INHERITANCE OF ALBINISM

Annie L. W. Roy, wife of Robert Roy, was one of a fraternity of twelve; three besides herself were albinos

Photograph from Dr. C. B. Davenport

In addition to these negative measures designed to reduce the birth rate among those with defective heredity, supporters of the eugenics social program also urge the alteration of social customs by which earlier marriage and a higher relative birth rate may be encouraged among the more able and gifted members of society.

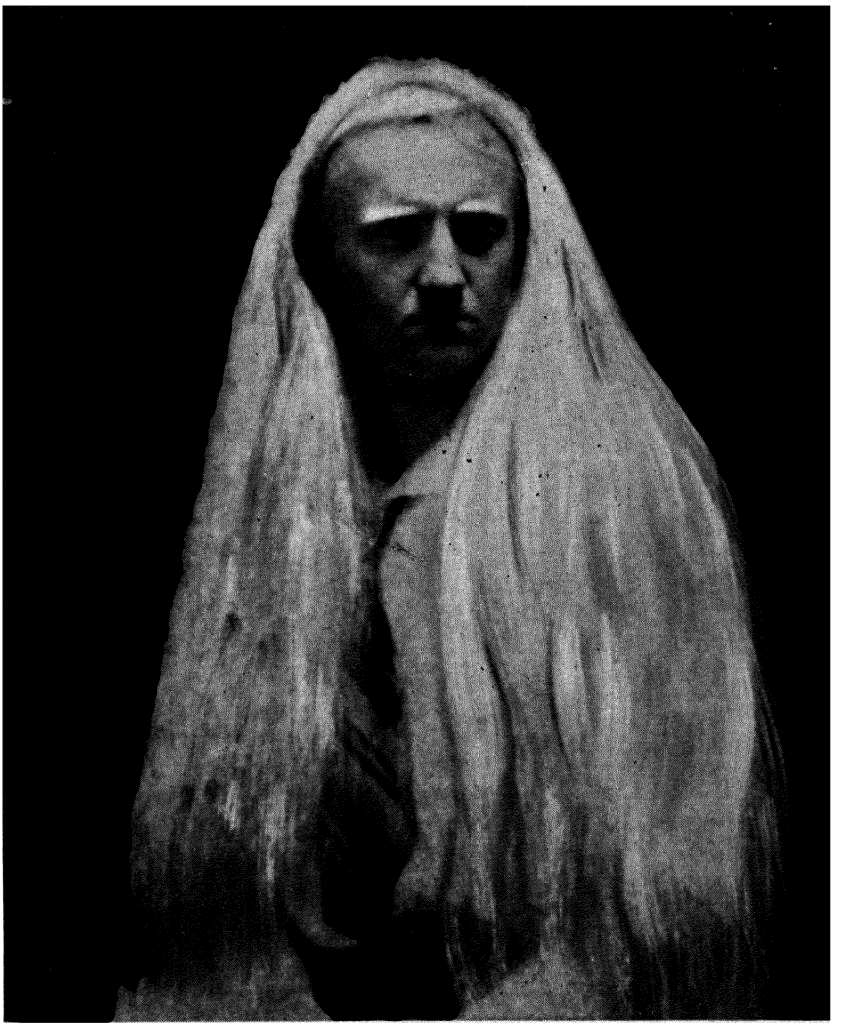


Fig. 47—THE INHERITANCE OF ALBINISM

King Charles Roy, the only child of Robert and Annie L. W. Roy, an albino born of albino parents. Albinism in man is inherited as a single recessive trait just as it is in other mammals

Photograph from Dr. C. B. Davenport

One measure now conceived as possibly effective toward this end is the spread of birth-control knowledge equally to all classes of society. This is now known and practised more by people of better education and intelligence, whereas if it were a part of the knowledge of every citizen to use or to disregard as he chooses, it would probably reduce the birth rate and increase the physical and mental health of many families which now suffer from too many children.

All of these proposals, and especially the last have engendered an opposition which has served to promote an active discussion and thus to create a demand for the full facts which must be known before far-reaching social decisions can be made intelligently.

Up to the present the negative measures advocated by eugenists have met with more success than the positive ones. Prevention of reproduction on the part of criminals, feeble-minded, and insane has made headway in several States even against the reluctance of legal and medical boards to enforce such additional infringements on individual liberty. On the whole, the importance of heredity in some of the extreme types of defect in insanity, idiocy, and feeble-mindedness, and the net benefit accruing to society from reducing their rate of reproduction, are becoming sufficiently recognized to weaken the reasonable objections which many people have had to the interference of society with the rights of its members. Modern society is increasingly assuming powers never before granted to it, and restrictive laws appear to be less difficult to enact, although they are still difficult to enforce. The assumption of some measure of social control over the biological character of the population which eugenics foresees, seems at present to be inevitable, at least in the United States. Those who recognize the nature of the biological factors involved but who still feel that the freedom of the individual is a good to be preserved may still hope to prevent the irruption of social, racial, and religious prejudice into the direction of this difficult and delicate problem. In addition to the restriction of reproduction on the part of certain classes of society, many supporters of eugenics have also favored measures such as selective restriction of immigration, which seek to entrench and increase the possessors

of those characteristics upon which the present state of so rests. Eugenics, although nominally an agency of social cha may thus become a conservative force for the preservatio the *status quo* and may thereby reduce that flexibility whi one condition of social progress.

The best function of eugenics has been to promote the covery and dissemination of knowledge of human heredity, although this activity has been occasionally hampered by tendency toward immediate application through social ac it has nevertheless pointed out important social probl Modern society has for too long neglected the thoughtful sideration of its biological basis. What, for example, are biological and social effects of celibacy or of late marriag the part of highly endowed members of society? What ind effects on the rate of reproduction are brought about by pov housing conditions, length of required period of education, e ization of professional opportunities and of political powe women and of men? Does not war, by its inevitable elimin of many of the ablest members, exert a most serious delete effect on the character of the population?

To these and similar questions the society of the future continually address itself, and for help it must turn to the of genetics and eugenics.

Heredity and Environment

What now of that subject of so many a debate—whi more important, heredity or environment? This questio Professor H. S. Jennings, of the Johns Hopkins University pointed out, is itself outmoded and now rather absurd. T two can never be opposed; they must continually co-opera influencing the nature of all living things. Whenever we s of differences as due to inheritance, we should always imp express the necessary fact—"provided the environment rer the same."

Most of the inherited characters of plants and an with which we have dealt do seem to be stable within the r of conditions which they ordinarily encounter, but this i no means sufficient evidence for assuming that the "chara as such is inherited.

What Do We Inherit?

What then do we really inherit? *Actually we receive from our parents two minute single cells containing an assortment of molecules of living substance—genes.* Some of these specify the kinds of reaction which shall take place between our bodies and minds and our surroundings. The end result of our development depends on both factors.

An example from horticulture should make this dependence clear. There is a kind of primrose which has red flowers when grown at ordinary temperatures, but white ones when grown in a hot greenhouse. This differs from a variety which has white flowers when grown at either the low or the high temperature, and a single gene determines the difference. Obviously, "red" is not inherited at all, but only the ability to produce red under a special set of conditions. We speak likewise of resistance to a specific disease as inherited, but what shall we say is inherited in an environment from which the disease itself is absent? What is inherited in every case is a potentiality to respond in a specific way to specific factors in our environment.

This mitigates a little the apparently gloomy conclusion toward which all results of studies of heredity seem to be driving us. This conclusion is that the individual, whether he be fruit-fly, mouse, or man, has but little freedom in determining his own fate. The limits to many reactions are set within the fertilized egg cell from which each of us arises. Our sex, color, and race, and many of our physical and mental peculiarities are settled for us long before birth, and these determine many of the details of our lives.

But it is not heredity only which limits our freedom; all conditions about us which affect our development and our lives seem also to act according to laws inherent in the structure of living and non-living matter. If we are to rebel at the dark determinism of heredity, let us kick over the traces of cause and effect as well, for here lies the real root of our discontent. In these days of too much human law, to be made subservient to natural laws, and moreover to share these laws with insects, with guinea-pigs, with mere plants, seems to many to be a blow to human pride which is not to be suffered in silence, and they resist with

vigor this assault on the sovereignty of man and the freedom of the will!

Yet to rebel at this point is to bite the very hand that feeds us. Just as by understanding the laws governing the physical world man has been able to place himself in a more satisfying relationship to the forces of nature, so by understanding the laws governing continuity and change in his own and in his captive species can he gather aid and comfort in his efforts to guide his own life and theirs.

SUGGESTIONS FOR FURTHER READING

Prepared by the Author

HEREDITY AND HUMAN AFFAIRS—*Edward Murray East* SCRIBNER
The author, an outstanding authority on heredity, summarizes, explains, discusses, and interprets facts and theories of heredity and relates them to the chief social and economic questions of the day.

LIVING ORGANISMS—*Edwin Stephen Goodrich* OXFORD
Discusses the nature of life, the processes of heredity, the foundations of evolutionary theory and allied problems and presents the evidence clearly and intelligently.

PRINCIPLES OF GENETICS—*Edmund Ware Sinnott* and *L. C. Dunn* MCGRAW-HILL
A standard elementary textbook in which the fundamental principles of genetics are simply presented. A feature of the book is the use of specific problems and questions for thought and discussion which make it possible for the reader to test his understanding of the principles.

EVOLUTION, GENETICS, AND EUGENICS—*Horatio Hackett Newman (Editor)* CHICAGO
A series of excerpts from the works of authorities on the subjects listed. Both sides of debatable questions are fairly presented. It is well organized and well knit together by the Editor.

PROMETHEUS: or, BIOLOGY AND THE ADVANCEMENT OF MAN
Herbert Spencer Jennings DUTTON
Sketches briefly and simply man's biological background, the Mendelian rule of inheritance, and gives the fairest and most readable presentation of the relation of heredity and environment.

BEING WELL-BORN: AN INTRODUCTION TO HEREDITY AND EUGENICS
Michael Frederic Guyer BOBBS
Furnishes a very complete background to the study of the subject and a very comprehensive statement of the reproductive processes of nature. Although not what might be called a "popular" treatment, the writing is clear and the language plain.

WILLIAM BATESON, F.R.S. NATURALIST—*Beatrice Bateson* MACMILLAN
Contains an interesting memoir of the life of an exceptional man, one of the pioneers in the study of heredity, and many of his addresses covering a wide range of topics.

EXPERIMENTS ON PLANT HYBRIDIZATION—*Gregor Mendel* (Pamphlet) HARVARD
This is a translation of the brief report which Mendel made to the Natural History Society in Brunn in 1865. It is not only the original source of modern ideas of heredity, but is a shining example of what a good scientific paper should be—brief, clear, readable and modest. It is still the best paper published in this field.

THE BIOLOGICAL BASIS OF HUMAN NATURE—*Herbert Spencer Jennings* NORTON
A full length exposition of the biological principles underlying human life, written for the intelligent layman. It is at once practical and critical and is infused with a general philosophical viewpoint about biology and human activity.

CRIME AND DESTINY—*Johannes Lange* BONI
A sound attempt to assess the environmental and hereditary factors leading to anti-social behavior, based on the author's study of pairs of twins at least one of which had been convicted of crime. The effect on the reader of the straightforward descriptions of the persons involved proves that human interest need not be lost through the employment of scientific methods and viewpoints.

KEY TO PUBLISHERS

BOBBS—Bobbs-Merrill Company, 724 N. Meridian Street, Indianapolis, Ind.
BONI—Albert & Charles Boni, Inc., 66 Fifth Avenue, New York, N. Y.
CHICAGO—University of Chicago Press, 5750 Ellis Avenue, Chicago, Ill.
DUTTON—E. P. Dutton & Co., Inc., 286-302 Fourth Avenue, New York, N. Y.
HARVARD—Harvard University Press, Randall Hall, Cambridge, Mass.
MCGRAW-HILL—McGraw-Hill Book Company, Pennsylvania Terminal Building, 370 Seventh Avenue, New York, N. Y.
MACMILLAN—The Macmillan Company, 60 Fifth Avenue, New York, N. Y.
NORTON—W. W. Norton & Company, Inc., 70 Fifth Avenue, New York, N. Y.
OXFORD—Oxford University Press, 114 Fifth Avenue, New York, N. Y.
SCRIBNER—Charles Scribner's Sons, 597 Fifth Avenue, New York, N. Y.

GLOSSARY

(Only those terms are defined in this glossary which either are not explained in the text or are explained once and are used again several pages from the explanation.)

ALBINO: a person or animal born with a deficiency or absence of the usual pigments in the skin, the hair, and the eyes.

ANTIBODY: any of various bodies or substances in the blood which tend to neutralize the action of harmful bodies, such as toxins or the bacteria which produce the toxins; example, antitoxins.

ASEXUAL REPRODUCTION: any process of reproduction which does not depend upon the production of single sexual cells (egg and sperm). Examples, reproduction by cuttings, from roots, or bulbs.

BACTERIA: a group of micro-organisms, widely distributed, occurring in air, water, and soil, as well as in the bodies of living animals and plants and in products derived from them.

BUDDING: a process of asexual reproduction in which a protruded part of an organism develops into a new organism; it may either break off or remain attached.

CHROMATIN: the deeply staining protoplasmic material found in the nucleus of a cell, which at cell division becomes aggregated into chromosomes.

CHROMOSOME: one of the small deeply staining bodies into which the chromatin of a cell nucleus resolves itself previous to cell division.

CYTOLOGIST: one who specializes in cytology, the branch of biology which treats of cells.

CYTOPLASM: the protoplasm of the cell exclusive of the nucleus.

DOMINANCE: the appearance of a character in a hybrid which contains only one gene for the character. Contrasted with recessiveness which means that the character is expressed only when two genes for it are present.

ENVIRONMENT: in biology, the aggregate of all the external conditions and influences affecting the life and development of an organism.

FISSION: reproduction by spontaneous division of the body into two equal parts.

GAMETE: a sexual cell, egg or sperm.

GENE: a hypothetical unit in the chromatin of the cell which has a specific influence on certain characteristics; the unit of hereditary transmission.

GENETICS: the science which deals with the laws of heredity and variation and the processes involved in the origin of species, races, and individuals.

GERMPLASM: the substance contained in the germ cells by which hereditary characters are transmitted.

HYBRID: the offspring of the union of two parents which differ in a heritable character or group of characters.

INBREEDING: breeding from a male and female of the same or very closely related parentage.

LETHAL: causing death.

LINKAGE: the tendency of two or more hereditary characters to remain together (or apart) in inheritance.

MICROCOSM: a miniature universe.

MUTATION: a sudden heritable change in some aspect of the organism, due to an alteration in the hereditary material. Frequently in the restricted sense of a sudden change in a gene.

NORM: the recognized average or standard condition.

NUCLEUS (plural nuclei): (from the Latin, meaning, "little nut or seed"), the central deeply staining body, with specialized structure and functions, found in nearly all cells.

OÖCYTE: a female germ cell before maturation; i.e., before its chromosomes have been reduced in number.

OÖGONIA (singular, oögonium) : the cells which give rise to the oöcytes; immature female germ cells.
ORGANISM : a living individual, plant or animal.
POLAR BODY : one of the minute, non-functional cells formed in the final stage of the maturation of the egg in animals.
PROTOPLASM : the living substance of which animals and plants are essentially composed.
PROTOZOAN (plural, protozoa) : a minute animal, generally consisting of a single cell, or of a colony, all the cells of which are alike.
RECESSIVE CHARACTER : a character which does not appear in the hybrid; but which requires two like genes to bring it to view.
SOMA : the body of any organism as contrasted with the germ cells.
SPERM : the male gamete or reproductive cell.
SPERMATID : one of the cells which arise by division of the spermatocytes and become spermatozoa.
SPERMATOCYTE : a cell which gives rise to spermatids; an intermediate stage in the maturation of the spermatozoa.
SPERMATOGONIUM (plural, spermatogonia) : one of the primitive male germ cells.
SPERMATOZOÖN (plural, spermatozoa) : a mature male sexual cell (the sperm cell) of an animal.
VESTIGIAL : pertaining to a small or imperfectly formed part or remnant of an organ.
YEAST : a minute unicellular fungus.
ZYGOTE : the product of the union of two sexual cells; hence the individual which arises from the fertilized egg.

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WITH PRONUNCIATIONS †

† For key to pronunciation, see page 120.
* Asterisk denotes illustration.

Key to Pronunciation

ā as in dāy
â " " senâte
ă " " ădd
å " " cåre
ä " " färˌ
ȧ " " låst

ē as in mēte
ê " " êvent
ĕ " " ĕnd
ē " " tērm

ġ = j (gentile)
ğ as in get

ī as in tīme
î " " îdea
ĭ " " ĭll
ī " " fīrm

ō " " ōld
ô " " ôbey

ŏ as in nŏt
ô " " lôrd

ū " " ūse
û " " ûnite
ŭ " " ŭs
û " " tûrn